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THE BRITISH LOWER JURASSIC SPECIES OF THE BIVALVE GENUS *CARDINIA*

C. P. PALMER

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GEOLOGY Vol. 26 No. 1
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THE BRITISH LOWER JURASSIC SPECIES OF THE BIVALVE GENUS *CARDINIA*

BY

CHARLES PHILIP PALMER

Pp. 1–44 ; 5 *Plates,* 9 *Text-figures*

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THE BRITISH LOWER JURASSIC SPECIES OF THE BIVALVE GENUS *CARDINIA*

By C. P. PALMER

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SUMMARY

Seven new species of *Cardinia* are described and sixteen others recognized in the British Lias. These are grouped under four informal, infra-generic groups: Deltoids, Ovoids, Concinnoids and Rugoids. The new species are *subabducta, raasayi, huntcliffensis, subobovata, tuffleyensis, dayi* and *tutcheri*. A list of the specific names available in the genus *Cardinia* is included. Neotypes of *Cardinia crassiuscula* (J. Sowerby) and *C. laevis* (Young & Bird) are designated. The hinge notation of *Cardinia* is discussed and shown to have been wrongly interpreted by previous workers. Discussion of the palaeoecology and evolution leads to the conclusion that the characteristic hinge of *Cardinia* was persistent throughout the range of the genus and that it was a strong mechanism for resisting shear action. This is taken to indicate that these bivalves were active shallow burrowers. Arguments are offered which suggest that the generic relations of *Cardinia* are with the Lucinacae rather than with the Crassatellacae, and that oxygen availability was the principal limiting factor controlling their distribution.

I. INTRODUCTION

THE NUMBER of species described under, or subsequently referred to, the genus *Cardinia* exceeds 120. This large and variable group of heterodont bivalves would, if it were living, cause no little concern to the neontologists – even with the living animal to assist in classification. Palaeontologists, with nothing but shell morphology to work on, demonstrate their perplexities in the extremes to which their systematic philosophies lead them.

Brauns, in 1871, with some 43 named forms to classify, placed them all in synonymy with J. Sowerby's three 'classic' species – *Cardinia concinna*, *C. crassiuscula* and *C. listeri*. On the other hand Hayami (1958) listed 111 names and recognized 75 of these as true species of *Cardinia*.

At the generic level five names were proposed for the group before Cox (1951) stabilized the genus *Cardinia* to date from Agassiz, 1841. Hayami grouped his 75 species into six unnamed subgeneric groups. For general purposes the majority of *Cardinia* species fall into four groups, three of which correspond with Brauns' three 'species'

(1) Deltoids : medium sized, more or less triangular forms centred on *C. listeri*.
(2) Ovoids : small more or less ovate forms with subcentral umbones, centred on *C. ovalis*.
(3) Concinnoids : large elongate forms with beaks on the anterior quarter, centred on *C. concinna*.
(4) Rugoids : ovoids with rugose growth lamellae, centred on *C. toriyamai*.

To many workers this grouping might suggest taxa of subgeneric level, but the present writer is not convinced that general outline alone is a sufficient basis for proposing formal supra-specific taxa. Nevertheless, these informal morphologically descriptive terms, deltoids, ovoids, concinnoids and rugoids, are useful in discussion and, lacking formal status, they avoid trinomialism and add nothing to the 'jungle of nomenclature'.

Work on the Middle Lias of the Dorset Coast (Palmer 1962) and of Gloucestershire (Palmer 1972) led to the discovery of three undescribed forms of *Cardinia*. One of these came from the Margaritatus Zone of Gloucestershire, the other two from the Margaritatus and Spinatum Zones of Dorset. The Gloucestershire specimens, though only 45 mm in length, resemble the equivalent growth stage of the stratigraphically higher *Cardinia concinna* but differ in their shorter length-to-height ratio and smaller size. The Dorset forms bear a remarkable resemblance to *Cardinia toriyamai* described by Hayami (1958) from the Lower Liassic Higashinagano Formation in Yamaguchi Prefecture, west Japan. The earliest of the Dorset shells were found together with many small immature bivalves in Day's Shell Bed, which lies a few feet below the better-known Starfish Bed at the top of the Eype Clay in the

Stokesi Subzone of the Margaritatus Zone (Howarth 1958). Attempts to match these shells with other specimens of *Cardinia* in the collection of Mesozoic bivalves in the British Museum (Natural History) proved futile, except for one specimen of *Cardinia rugulosa* Tate 1875, from Munger Quarry, Radstock, and two others collected by J. W. Tutcher and J. Etheridge from the Spinatum Zone, in the Marlstone Layer of the Junction Bed, Dorset. The last resembled no previously described European forms of *Cardinia* and differed only slightly from the stratigraphically older Shell Bed specimens and those from Radstock.

The 23 species of *Cardinia* recognized as occurring in the British Lias are grouped in four categories according to their general appearance. Hayami (1958 : 117–118) divided the genus into six groups, prefixing each with the characteristic species of that group (e.g. 'Concinna-group', 'Crassissima-group' etc.). The number of divisions seems extravagant when apparently four will suffice, at least for the British species which are listed as follows

DELTOIDS

Cardinia with a more or less trigonal outline corresponding with Hayami's 'Hybrida-group'. They include the following British species :

C. listeri (J. Sowerby 1817), Lower Sinemurian	Pl. 1, figs 1–3
C. hybrida (J. Sowerby 1817), Hettangian–Sinemurian	Pl. 1, figs 5–8 ; Pl. 3, fig. 7
C. imbricata (Stutchbury 1842), Sinemurian	Pl. 1, figs 11–13
C. subabducta sp. nov., Sinemurian	Pl. 1, figs 9–10
C. raasayi sp. nov., Upper Sinemurian	Pl. 1, fig. 4
C. ingens Tawney 1866, Hettangian	Pl. 5, fig. 7
C. crassissima (J. Sowerby 1817), Upper Domerian	Pl. 4, figs 1–2
C. idalia d'Orbigny 1850, Upper Domerian	Pl. 4, fig. 3
C. slatteri Wilson & Crick 1889, Lower Whitbian	Pl. 5, figs 8–10

(*Nidarica* Cox (1961 : 335), proposed for *C. slatteri*, is treated as a synonym of *Cardinia* below and *slatteri* is here grouped with the deltoids.)

OVOIDS

Cardinia with ovate outline corresponding, in part, with Hayami's 'Toriyamai-group'. They include the following British species :

C. crassiuscula (J. Sowerby 1817), Lower Sinemurian	Pl. 2, figs 7–10
C. ovalis (Stutchbury 1842), Hettangian	Pl. 2, figs 1–3
C. huntcliffensis sp. nov., Domerian	Pl. 3, fig. 8
C. laevis (Young & Bird 1828), Domerian	Pl. 3, figs 4–6
C. subobovata sp. nov., Hettangian	Pl. 4, fig. 6
C. suttonensis Tawney 1866, Hettangian	Pl. 5, fig. 6

CONCINNOIDS

Elongated *Cardinia* corresponding with Hayami's 'Concinna-group' but, owing to his wrong citation of type species of *Cardinia* (1958 : 117), they are not '*Cardinia* sensu stricto' of his own classification. The British species are :

C. concinna (J. Sowerby 1819) Upper Domerian–Lower Whitbian	Pl. 3, figs 1–2
C. gigantea (Quenstedt 1856), Lower Sinemurian	Pl. 3, fig. 3
C. lanceolata (Stutchbury 1842), Lower Sinemurian	Pl. 2, fig. 4
C. attenuata (Stutchbury 1842), Carixian	Pl. 2, figs 5–6
C. tuffleyensis sp. nov., Domerian	Pl. 4, figs 4–5

RUGOIDS

Cardinia with ovate outline and imbricating growth lamellae, some with upturned edges. These correspond, in part, with Hayami's 'Toriyamai-group' and include the following British species :

C. rugulosa (Tate 1875), Carixian	Pl. 5, fig. 5
C. dayi sp. nov., Lower Domerian	Pl. 5, fig. 3
C. tutcheri sp. nov., Upper Domerian	Pl. 5, figs 1–2

TABLE

The stratigraphical zones and stages of the British Lias proposed by Dean, Donovan & Howarth (1961) and used in this study

ZONES	STAGES	LITHOLOGY		
Levesquei Thouarsense	Yeovilian (Upper Toarcian)	Sands and marls	Upper Lias	
Variabilis Bifrons Falciferum	Whitbian (Lower Toarcian)	Shales and marls passing southwards into thin limestones and nodules		
Tenuicostatum		Transition Bed		
Spinatum	Domerian (Upper Pliensbachian)	Marlstone Rock Bed	Middle Lias	Middle Lias of some 19th century authors
Margaritatus		Sandy shales		
Davoei Ibex Jamesoni	Carixian (Lower Pliensbachian)	Silty shales		
Raricostatum Oxynotum Obtusum Turneri Semicostatum Bucklandi	Sinemurian	Marls and shales Frodingham Ironstone Shales and paper-shales	Lower Lias	
Angulata Liasicus Planorbis	Hettangian	Shale and limestone alternations – 'Blue Lias'		

The Table shows the stratigraphical zones and stages of the British Lias used in this study. The column headed 'Lithology' is generalized and simplified but usually the lowest four zones are in limestone and shale alternations – a division usually known as the 'Blue Lias'. This is succeeded by paper-shales and shales around the Semicostatum and Turneri Zones. The rest of the Lower Lias is in shale and marl which becomes more silty around the Davoei Zone, and sandy in the Margaritatus Zone of the Middle Lias. The Marlstone Rock Bed is widespread and corresponds with a profound change in the Liassic fauna. The succeeding Transition Bed marks the highest reliable record of British *Cardinia*.

II. TRIVIAL NAMES USED WITH *CARDINIA*

In proposing new names for *Cardinia* species the following trivial names were discovered to have previously appeared in publication in combination with the generic name *Cardinia*. It is basically Hayami's list (1958 : 123–127) but with additions by the present author. No claim is made for its completeness but only that these names at least can be avoided by other workers. New species described herein are indicated *.

abductus
acuminata
amurensis
amygdala
andium
angustata
angustiplexa
antiqua
aptychus
aritiensis
attenuata
authelini

bensoni
breoni
brevis

chillyensis
collenoti
concinna
conjugensis
contracta
copides
cordata
crassissima
crassiuscula
cuneata
cyprina

**dayi*
densistriata
depressa
deshayesi
desoudini
dormali
dunkeri

elliptica
elongata
eveni
exigua
exilis

fischeri
follini

gibba
gibbosula
gibbosum
gigantea
gleimi
gottingensis

hennocquii
**huntcliffensis*
hybrida

idalia
imbricata
inexpectans
infera
ingelensis
ingens
insignis
itea

keuperiana
koninckii
kullensis

laevis
lamellosa
lanceolata
latiplex
latitruncata
lerichei
listeri
lucinaeformis
lycetti

mactroides
minor
misawensis
moreana
morisi

nachamensis
nilssoni
nostra

oblonga
obovata
oppeli
ovalis
ovula
ovum

philea
piriformis
plana
ponderosa
porrecta

quadrangularis
quadrata

**raasayi*
regularis
rhyckholti
rugulosa

scapha
scutula
securiformis
siberica
similis
sinemuriensis
slatteri
**subabducta*
subacuminata
subaequilateralis
subangulata
sublamellosa
**subobovata*
subovalis
subtrapezoides
sulcata
suttonensis

tas-aryensis
toriyamai
trapezium
triadica
trigona
**tuffleyensis*
**tutcheri*

unioides

wyomingensis

zeilleri

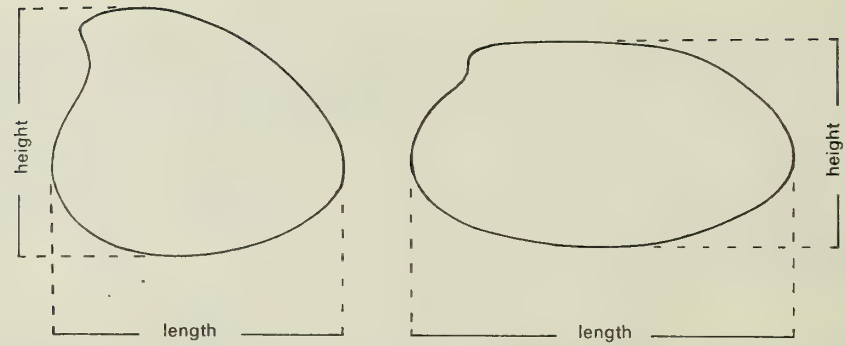

FIG. 1. Measurements of *Cardinia* : left figure a deltoid, right figure a concinnoid. Length is measured along the longitudinal axis, i.e. the greatest distance between the anterior and posterior margins. In *Cardinia* the longitudinal axis is usually parallel to a line joining the anterior and posterior laterals. Height is measured at right angles to the length.

III. HINGE NOTATION

The internal structures forming the hinge of *Cardinia* are remarkably constant in position and character. The typical pattern comprises in the right valve a more or less obsolete cardinal tooth 3b, usually no more than an elongated low swelling,

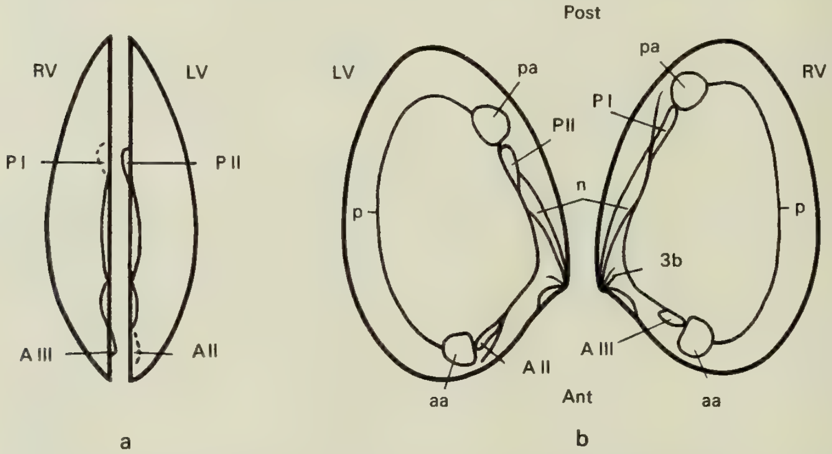

FIG. 2. (a) Articulation of the lateral teeth in the valves of *Cardinia crassiuscula* drawn, with the dorsal margin uppermost, from specimens from the Frodingham Ironstone of Scunthorpe, Lincolnshire, $\times \frac{1}{2}$. The dotted teeth lie ventral to teeth with solid lines. (b) Internal left and right valves of *C. crassiuscula* from the Frodingham Ironstone of Scunthorpe, Lincolnshire, $\times \frac{1}{2}$. Symbols for both figures are as follows : LV, left valve ; RV, right valve ; Ant, anterior ; Post, posterior ; n, ligamental nymph ; p, pallial line ; aa, anterior adductor muscle scar ; pa, posterior adductor muscle scar ; 3b, position of obsolescent cardinal tooth ; AII, anterior lateral tooth in left valve ; AIII, anterior lateral tooth in right valve ; PI, posterior lateral tooth in left valve.

well-developed lateral teeth consisting of an anterior lateral tubercular tooth, and a posterior lamellar tooth forming a socket between itself and the edge of the shell. In the left valve there is a depression to receive the obsolescent cardinal 3b but no trace of other cardinals, an anterior lateral forming a socket between itself and the edge of the shell to receive the anterior lateral in the right valve, and a posterior lateral tubercular tooth which fits into a socket formed by the posterior lateral tooth and the edge of the shell in the right valve.

Cox (1961 : 327, fig. 1) published a figure of the internal dentition of *C. hybrida* and reproduced Douvillé's (1921 : 117–118) application of the Munier-Chalmers–Bernard (1895) hinge notation to *Cardinia.* Cox remarked (p. 328) that the upper anterior lateral in the right valve, AIII of Douvillé, was not recognizable by him in the specimens he had examined, a statement which is entirely supported by the present author's experience. Douvillé depicts two anterior laterals and notates them AI and AIII ; the last, if it does not correspond to the edge of the shell, is entirely imaginary. In order to discover the relationships of the anterior and posterior laterals several complete and articulated specimens of *C. hybrida, C. concinna* and *C. ovalis* were sectioned so that the plane of the cut passed vertically through the laterals. These sections revealed the unsatisfactory state of Douvillé's application of the Bernard hinge notation since, in all cases, AII in the left valve was ventral to AI in the right. The numbering of lateral teeth should begin with the lowest (most ventral) tooth upwards (Cox 1969 : N53). Hence the anterior lateral in the right valve should be designated AIII (= AI of Douvillé) and Douvillé's 'AIII' does not exist, or it corresponds with the edge of the shell.

In the right valve the posterior lateral is ventral to the tubercular tooth PII in the left valve and it is correctly designated PI by Douvillé, but no tooth, unless it be

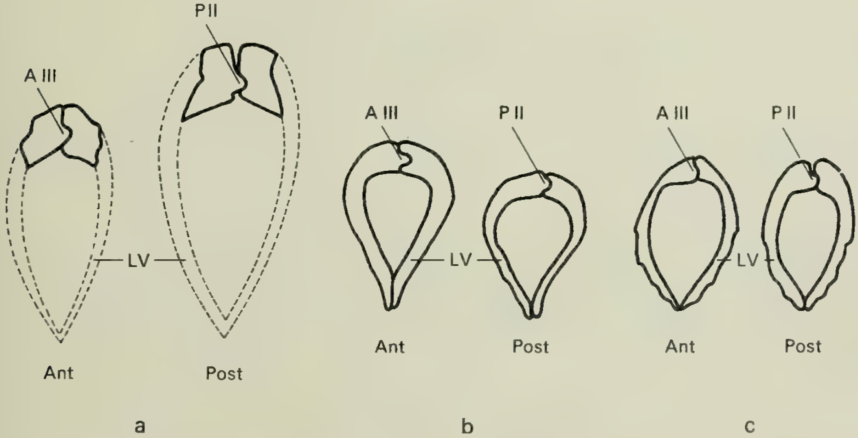

Fig. 3. Sections through lateral teeth of :
(a) *Cardinia concinna* from the Margaritatus Zone of Stonehouse, Gloucestershire.
(b) *C. attenuata,* locality and horizon unrecorded ; B.M.(N.H.) duplicate collection.
(c) *C. ovalis,* locality and horizon unrecorded. B.M.(N.H.) duplicate collection.
Notation as for Fig. 2. × ½.

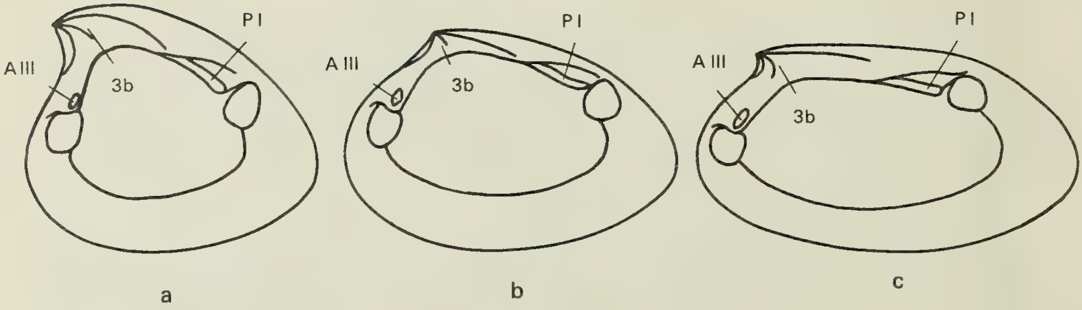

FIG. 4. Comparative hinges of right valves of :
(a) *Cardinia listeri*, Sinemurian of Evesham, Worcestershire.
(b) *C. ovalis*, Hettangian of Chadbury, Worcestershire.
(c) *C. concinna*, Whitbian, Transition Bed, Astrop, Northamptonshire.
The constancy of the dentition is well demonstrated, in spite of difference of stratigraphical age in 4b and 4c, and difference of shape in 4a and 4c. Notation as for Fig. 2. × $\frac{1}{2}$.

the edge of the shell, is visible above PI, hence the 'PIII' of Douvillé does not exist. Unfortunately Douvillé failed to reveal the fact that in *Cardinia* the lateral teeth and sockets alternate, the anterior right tooth fitting into the anterior left socket, and the posterior left tooth into a posterior right socket. This arrangement forms a very powerful shear-resistant articulation for the two valves, and its permanence throughout the stratigraphical range of the genus argues for powerful selective forces maintaining this unique form of hinge.

IV. BRITISH LIASSIC SPECIES OF *CARDINIA*

Family **CARDINIIDAE** Zittel 1881

Genus ***CARDINIA*** Agassiz 1841

(= *Thalassides* Berger 1833, suppressed I.C.Z.N. ; *Ginorga* Gray 1840, *nom. nud.* ; *Sinemuria* de Christol 1841, suppressed I.C.Z.N. ; *Pachyodon* Stutchbury 1842 ; *Dihora* anon. 1842 ; *Storthodon* Zittel 1881 ; *Nidarica* Cox 1961.)

TYPE SPECIES. *Unio listeri* J. Sowerby 1817, designated I.C.Z.N. Opinion 292. The generic name was validated in the same opinion (see Cox 1951).

DIAGNOSIS. Integripalliate heterodont bivalve molluscs with unique hinge consisting of anterior laterals AII and AIII, posterior laterals PI and PII, and an obsolescent cardinal 3b.

REMARKS. The genus *Nidarica*, proposed by Cox (1961), type species *C. slatteri* Wilson & Crick 1889, is here considered to be a synonym of *Cardinia* Agassiz 1841. The external shell features distinguishing it from other cardiniids, concave lateral surfaces and very incurved beaks, are only an extension of a trend already visible in the earlier deltoid *C. idalia* d'Orbigny. The hinge differs in no significant way from that of other species of *Cardinia*.

Cardinia listeri (J. Sowerby 1817)

Plate 1, figs 1–3

1817 *Unio listeri* J. Sowerby : 123, pl. 154, figs 1, 3, 4.
1842 *Pachyodon listeri* (Sowerby) Stutchbury : 482, pl. 9, figs 1, 2.
1849 *Cardinia listeri* (Sowerby) Brown : 213, pl. 74, fig. 20 (only).
1962 *Cardinia listeri* (Sowerby) Castell : 64, pl. 10, fig. 2.

MATERIAL. In the British Museum (Natural History) are two syntypes : one corresponding to Sowerby's fig. 1 'sent me from Durham, as found in that neighbourhood some years since in Clayey Limestone' ; and another, fig. 4, collected by a Mr Strangeways from Scarborough. Since Lias is known at neither of these localities the following explanations are offered. Specimens resembling the syntypes were collected by J. F. Blake from the Bucklandi Zone of Redcar, Yorkshire. Redcar is but 20 miles from Durham and a collector living in that city might have visited Redcar and sent the specimen collected to Sowerby 'from Durham'. Around Scarborough Middle and Upper Jurassic is overlain by Boulder Clay which seems to have been a rich source for Jurassic fossils – and possibly of Sowerby's other syntype. The specimen corresponding to Sowerby's pl. 154, fig. 1 (the 'Durham' specimen) is here selected lectotype leaving the other (the 'Scarborough' specimen) as paralectotype. Dimensions of lectotype, B.M.(N.H.) Pal. Dept. LL 31297 : height 44 mm ; length 50 mm ; inflation 23 mm ; $h/l = 87{\cdot}5\%$ (Pl. 1, fig. 1). Dimensions of Paralectotype, B.M.(N.H.) 43221 : height 40 mm ; length 50 mm ; inflation 21 mm ; $h/l = 80{\cdot}0\%$ (Pl. 1, fig. 2).

DESCRIPTION. Sowerby's description is 'cordate, transversely imbricated, beak recurved, acute ; posterior side small ; middle flattish ; shell thick'. The types are subtrigonal in outline, slightly prosogyrous, beaks on the anterior quarter of the length ; shell moderately inflated with the anterior margin slightly concave. The shell is covered with about 18 fairly regularly spaced, concentric growth imbrications between shell heights 8 mm and 44 mm.

The hinge consists of a massive and strongly arched hinge plate containing, in the right valve, an obsolescent cardinal tooth 3b, a tubercular anterior lateral AIII, and an elongated posterior lateral PI making a socket for the reception of the posterior lateral tooth of the left valve. The left valve contains a barely perceptible fold for the reception of 3b of the right valve ; a tubercular anterior lateral AII forms a socket, with the edge of the shell, for the reception of AIII in the right valve ; an elongated and tubercular posterior lateral PII fits into a socket formed in the right valve by PI and the edge of the shell. A deeply sunk ligamental nymph lies posterior to the beaks and above the summit of the arch formed by the hinge plate.

Both the anterior and posterior adductor muscle scars are fairly well impressed, causing the ends of the hinge plate to be abruptly truncated and terminating in a vertical wall from the top of the hinge plate down to the muscle scar. An entire pallial line is usually well displayed and makes a regular curve from the anterior adductor towards the posterior adductor, which it passes ventrally, curving sharply back to meet it from a postero-ventral direction. A rather deeply impressed lunule lies beneath the incurled beaks.

COMPARISONS. This differs from *C. hybrida* in its more elevated shell, and from *C. raasayi* sp. nov. in its flatter ventral margin and smoother shell.

HORIZON AND LOCALITIES: Range probably Bucklandi–Obtusum Zones in the Sinemurian Stage. It has been reported from: 1·2 km (¾ mile) west of Watchet, Somerset; Cheltenham and Stonehouse (not the quarry), Gloucestershire; Bengeworth and Evesham, Worcestershire; Warkworth and Welford, Northamptonshire; in the Frodingham Ironstone at Scunthorpe, Lincolnshire; Redcar, Yorkshire.

Cardinia hybrida (J. Sowerby 1817)

Plate 1, figs 5–8: Plate 3, fig. 7

1817 *Unio hybrida* J. Sowerby: 124, pl. 154, fig. 2.
1833 *Unio depressa* Zieten: 81, pl. 61, fig. 1a–d.
1842 *Pachyodon cuneatus* Stutchbury: 484, pl. 10, figs 11, 12.
1842 *Pachyodon hybrida* (Sowerby) Stutchbury: 482, pl. 9, figs 3, 4.
1849 *Cardinia listeri* (Sowerby) Brown: 214, pl. 74, fig. 19 (only).
1962 *Cardinia hybrida* (Sowerby) Castell: 64, pl. 10, fig. 2.

MATERIAL. Sowerby's holotype, fig. 2, B.M.(N.H.) 43222, is recorded by him from Nottinghamshire, whence it came either from the Lower Lias or from Boulder Clay. If the latter, then comparison with specimen B.M.(N.H.) L 28722, from Robin Hood's Bay, a block with three specimens exposed, indicates that the origin may have been Yorkshire. Dimensions of holotype, B.M.(N.H.) 43222: height 28 mm; length 42 mm; inflation 15 mm (crushed); $h/l = 66{\cdot}5\%$ (Pl. 1, fig. 5).

DESCRIPTION. Sowerby's terse description is: 'oblong, ovate, anterior side subacuminate; surface imbricated; breaks recurved, acute; shell thick', and needs little amplification except to add that the imbricating lamellae are slightly undercut, the posterior often pointed, and the lunule rather deeply excavated and, in some cases, bounded by a ridge. The hinge teeth are exactly as in *C. listeri* only smaller, and the hinge plate, owing to the more depressed outline of the shell, forms a flatter arch.

COMPARISONS. Zieten's *Unio depressa*, from the Upper Sinemurian and Lower Pliensbachian of Deyerlock and Vaihingen near Stuttgart, Württemberg, is a slightly more depressed form of *C. hybrida*. In Britain it occurs most abundantly in the Lower Lias of Gloucestershire and Worcestershire where it shows complete gradation into the true *hybrida*-form. *C. hybrida* differs from *C. listeri* in being consistently more depressed with a h/l ratio of 66·5% compared with 87·5% in *C. listeri*. *C. depressa* (Pl. 1, figs 7–8) is here treated as a variety of *hybrida*.

Stutchbury's *Pachyodon cuneatus*, here figured on Pl. 3, fig. 7, is indistinguishable from *C. hybrida*. The type is from the 'Lias of Fretherne, Gloucestershire' and the species is recorded from bed 12 by Richardson (1908) which is but 150 cm (5 ft) below a limestone yielding *Arnioceras bodleyi*. This, together with the detailed work of Henderson (1934), confirms that it came from the Semicostatum Zone.

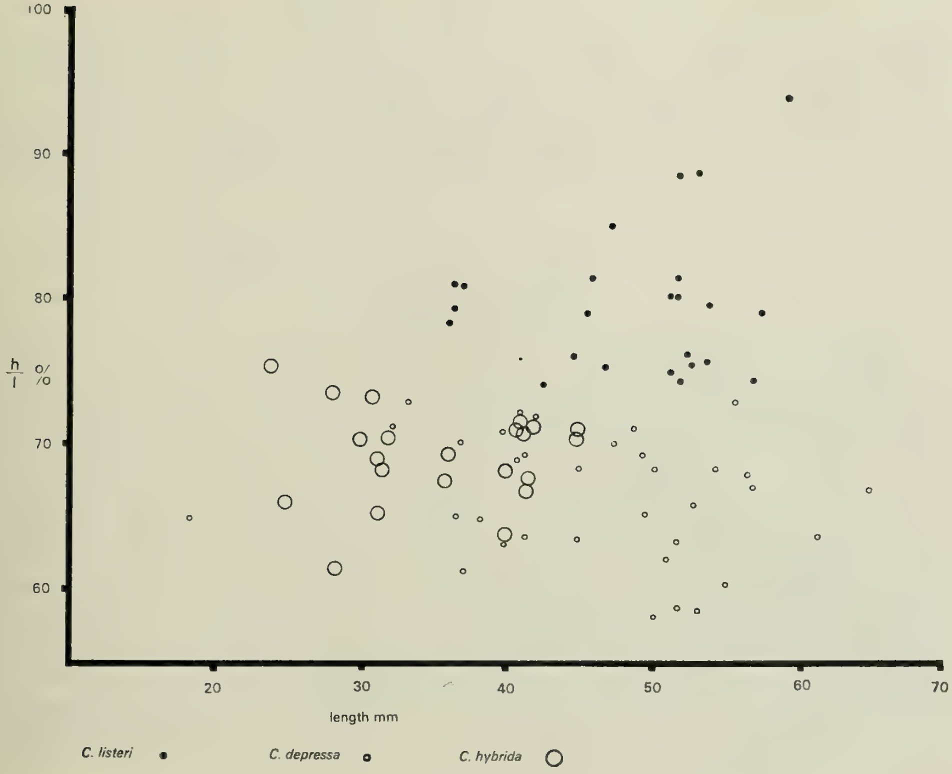

FIG. 5. The relationships of the three forms *Cardinia listeri, C. depressa* and *C. hybrida* expressed by their height : length ratios. *C. listeri* has a scatter distribution wholly above that of the *depressa–hybrida* group. Generally, *C. depressa* attains a larger size than *C. hybrida* and it is then that it assumes its characteristic shape. h/l % = height as a percentage of the length in Figs 5–8.

The stratigraphical horizon is confirmed by the B.M.(N.H.) specimen L 28721, from Redmile, Leicestershire, which is preserved in a block of Frodingham Ironstone, assigned by Hallam to the Semicostatum–Obtusum Zones, and which closely resembles Stutchbury's type figure. *C. listeri* (J. Sowerby) is a tall shell and *C. depressa* (Zieten) is, as the trivial name implies, depressed. Inevitably some *C. listeri* are less tall and some *C. depressa* are less depressed. *C. hybrida* seems to be just a smaller version of *C. depressa* and the two form a graded series. Hence a collection of these deltoids gives the impression of being 'all the same species', that is they are morphologically diverse but constitute a graded series. In order to test whether or not this was the case a height–length ratio graph was constructed and the dimensions of all available specimens, identified by conventional method of judgement, were entered upon it. Fig. 5 shows from left to right increasing length and from bottom to top increasing 'tallness' (height/length percentage) of shells.

It is clear that the *listeri* distribution lies wholly above the *hybrida–depressa* gradation.

Horizons and Localities. Range, probably Upper Angulata Zone in Hettangian Stage (Worcestershire) to Raricostatum Zone in Sinemurian stage (Scotland). Recorded from Gloucestershire ; Wilmcote and Binton, Warwickshire ; Fladbury, Bengeworth and Honeybourne, Worcestershire ; Redmile, Leicestershire ; Redcar, Yorkshire.

Cardinia imbricata (Stutchbury 1842)

Plate 1, figs 11–13

1842 *Pachydon imbricatus* Stutchbury : 483, pl. 9, figs 5, 6.

Material. Holotype in City Museum, Bristol, reg. no. C 2151, and two right valves in B.M.(N.H.). Dimensions of figured specimen, B.M.(N.H.) L 78419 : height 26 mm ; length 36 mm ; inflation 18 mm ; $h/l = 73\%$ (Pl. 1, fig. 11).

Description. 'Shell subtriangular ; lines of growth thin-edged, imbricated and numerous ; lunule cordate ; height 1·1, length 1·5, thickness 0·7. Lias, Banks of Severn, Gloucestershire, and Bishport, Somersetshire' (Stutchbury 1842 : 483). This is ovately trigonal in outline with a convex dorsal and ventral margin and a straight anterior descending rather steeply from the prosogyrous beaks. The shell surface is covered with numerous closely spaced, thin, imbricating lamellae. Lunule rather deeply excavated and bounded by a sharp ridge. Hinge as in *C. listeri*.

Comparisons. The species differs from *C. listeri* in the more closely spaced growth imbrications, the flatter anterior margin and the more convex dorsal outline giving it a 'hump-backed' appearance.

Horizon and Localities : ? Bucklandi–Semicostatum Zones in Sinemurian Stage ; Gloucestershire–Somersetshire. Recorded from Bishport, Somerset ; Fretherne and Hatherley railway cutting 2·4 km (1½ miles) south-west of Cheltenham, Gloucestershire.

Cardinia subabducta sp. nov.

Pl. 1, figs 9, 10

1842 *Pachyodon abductus* (Phillips) Stutchbury : 484, pl. 10, figs 9, 10 (non *Unio abductus* Phillips 1829).

Specific name. Alluding to *Pachyodon abductus* (Phillips 1829).

Material. Holotype in City Museum, Bristol, reg. no. C 2158, and one specimen, L 382, in B.M.(N.H.). Dimensions of L 382 : height 28 mm ; length 38 mm ; inflation 16 mm ; $h/l = 74\%$ (Pl. 1, fig. 9).

Diagnosis. Deltoid *Cardinia* resembling *C. listeri* but differing in its flatter dorso-ventral outline, sharper and less incurled beaks, and more acutely rounded anterior.

Description. Distinctly trigonal in outline with acutely pointed beaks, hardly incurled, and placed on the anterior quarter of the length. The postero-dorsal margin is nearly flat and meets the slightly convex venter on a sharply rounded posterior curve. The anterior is more broadly rounded than the posterior, becoming concave at the rather deeply impressed lunule. Hinge exactly as in *C. listeri*. Shell surface covered with close and regularly spaced growth halts.

COMPARISONS. Differs from *C. listeri* in its flatter postero-dorsal margin, sharper and less incurled beaks, and more acutely rounded anterior. From *C. hybrida* it differs in being more elevated, more trigonal in outline, and having a flatter dorsum.

REMARKS. Stutchbury (1842 : 484) mistakenly believed his *Pachyodon abductus* to be the same as Phillips' *Unio abductus* – an Inferior Oolite *Gresslya*. Stutchbury consequently recorded this from the 'Inferior Oolite, Dundry Hill, Somersetshire' and from the 'Lias, near Cheltenham'. This misidentification, together with the misidentification of the Marlstone at Cropredy as 'Inferior Oolite', is responsible for the long-held belief that the genus *Cardinia* ranged up into the Inferior Oolite. Although the specific name is not preoccupied in either *Pachyodon* or *Cardinia*, article 49 of the I.C.Z.N. Code requires that a new name be applied to this otherwise well-known form.

HORIZON AND LOCALITIES. Stutchbury (1842 : 484) records it from the 'Lias near Cheltenham'. The B.M.(N.H.) specimen, L 382, is labelled 'Lower Lias of Gloucestershire, Tennant Colln' and is associated with an older label reading 'Lower Lias, Evesham'. Attached to the specimen is a *Gryphaea* belonging to the *G. obliquata* group and this, together with the Evesham locality, suggests that it came from a horizon high in the Angulata Zone or low in the Bucklandi Zone, Hettangian to Sinemurian stages. Gloucestershire and Worcestershire seem to be the known limits of its distribution.

Cardinia raasayi sp. nov.

Plate 1, fig. 4

1843 ? *Cardinia laevis* Agassiz : 226, pl. 12″, figs 13–15 (non *Cardita laevis* Young & Bird 1826).

SPECIFIC NAME. From the island of Raasay.

MATERIAL. Holotype, B.M.(N.H.) L 76713, sole specimen from the island of Raasay, Inverness-shire, Scotland. Dimensions : height 50 mm ; length, 63 mm ; inflation, 27 mm ; $h/l = 79{\cdot}5\%$.

DIAGNOSIS. Deltoid *Cardinia* resembling *C. listeri* but differing in its more convex ventral margin, less incurled and more prominent umbones, and a shell surface lacking the prominent growth halts of typical *C. listeri*.

DESCRIPTION. Ovately trigonal outline with broadly convex ventral margin ; umbones prominent and beaks incurled and placed on the anterior quarter of the length ; lunule excavated beneath the incurled beaks ; shell surface covered with closely spaced plications and a few widely spaced, faint growth halts. Internal characters not seen.

COMPARISONS. This species can only be compared with *C. listeri*, which it closely resembles but from which it differs in the characters cited above. Its distinct shape and higher stratigraphical horizon indicate that it should be regarded as a separate species. Nevertheless, the holotype is the only example known to the author and it is impossible to say if the range of variation of the species and that of *C. listeri* might not overlap.

HORIZON AND LOCALITY. Raricostatum Zone in the Sinemurian Pabba Shales; banks of Allt Fearns, Raasay, Inverness-shire.

Cardinia ingens Tawney 1866

Plate 5, fig. 7

1866 *Cardinia ingens* Tawney: 86, pl. 4, fig. 2.

MATERIAL. Holotype in Institute of Geological Sciences, London, 91989. No other material seen; specimen not well enough preserved for measurement.

DESCRIPTION. The type is an internal mould of a relatively large deltoid, and Tawney claimed (p. 86) 'that the shell was crumbly but showed strong concentric folds of growth. It approaches nearest to *C. crassissima* of Agassiz' (non Sowerby). This species, together with his *C. suttonensis*, is from the Sutton Series of south Wales and the horizon is probably low in the Hettangian.

With only a poorly preserved internal mould to hand it is impossible to describe this form or to identify, or compare, it with any described species. The mould has two prominently raised muscle platforms indicating that the adductors were deeply set into the shell. The pallial line is clearly seen, but the hinge area is covered with a secondary growth of crystals. Until better preserved material is available this species must remain in abeyance as a *nomen dubium*.

HORIZON AND LOCALITY. Hettangian, Sutton Stone, Planorbis–Liasicus Zone; Llangan, near Brocastle, Glamorgan, south Wales.

Cardinia crassissima (J. Sowerby 1817)

Plate 4, figs 1, 2

1817 *Unio crassissimus* J. Sowerby: 121, pl. 153.
1849 *Cardinia crassissima* (Sowerby) Brown: 214, pl. 74, fig. 8.

MATERIAL. Holotype, one left valve, B.M.(N.H.) 43219, and other examples in B.M.(N.H.). Dimensions of holotype: height 62 mm; length 88 mm; inflation 38 mm; $h/l = 70{\cdot}5\%$ (Pl. 4, fig. 1).

DESCRIPTION. Sowerby's description is 'Ovate, transversely undulated or imbricated; beak recurved, acute posterior [i.e. anterior] side obscurely subcuneiform; shell very thick'. The dorsal outline is evenly convex and, like *C. imbricata*, has a 'hump-backed' appearance. The ventral margin is relatively flatter and passes, in an even curve, into the steeply sloping and short anterior. The strongly prosogyrous beaks lie on the anterior ninth of the length and are slightly incurled over a slightly excavated lunule.

COMPARISONS. From *C. idalia* and *C. listeri* it differs in its more depressed and ovate outline and the absence of a strong posterior carina. From *C. idalia* it differs in its lesser inflation and relatively flatter valves.

DISCUSSION. Examination of Sowerby's holotype leaves no doubt that Stutchbury (1842) confused two different forms when he identified his pl. 9, fig. 7 with Sowerby's *Unio crassissimus*. Stutchbury's specimen is the *C. idalia* of d'Orbigny, a form which is completely distinct from, and cannot be united with, *C. crassissima*. *C. idalia* is trigonal in outline and like a large *C. listeri*, but with a prominent angle in the postero-dorsal region ; it occurs in the Marlstone of Gretton, Gloucestershire (see p. 18). *C. crassissima* is depressed, ovate and with prosogyrous beaks ; specimens in the B.M. are labelled 'Marlstone, Tail's Hill, Glos.' (Tail's Hill is near Dursley). Another specimen, B.M.(N.H.) 20166e *ex* Baker Collection, is labelled 'Middle Lias, ? Bugbrook, Northants'. If this locality is correct then the matrix, which resembles that of the Transition Bed, suggests that the range should be extended from the Spinatum up to the Tenuicostatum Zone.

The stratigraphical position of Sowerby's holotype cannot be determined from his text, which only reveals that he received it from a Dr Sutton of Norwich who gave him 'many specimens of Fossil shells as British, *without localities* [my italics–C. P. P.] among which are several of this species all formed of Carbonate of Lime'. It was Parkinson who told Sowerby (1817 : 121) that these fossils 'are usual in Gloucestershire and Wiltshire, near Bath, sometimes in the Lias Clay', but since he was not specifically referring to Sowerby's specimen the origin must remain unknown. The only specimen known of similar preservation came from Tail's Hill, near Dursley, Gloucestershire.

Placing *C. crassissima* among the deltoids requires some explanation since it clearly presents a markedly ovate outline. The umbones of ovoids are usually placed between the median line and the anterior third, as in *C. ovalis* and *C. crassiuscula*. In contrast the deltoids usually have terminal or subterminal beaks and are strongly prosogyrous. *C. crassissima* has subterminal beaks and it is therefore included in the deltoids.

HORIZON AND LOCALITIES. Marlstone, Spinatum Zone, Domerian Substage. Adults are recorded from Tail's Hill near Dursley, Gloucestershire ; Bugbrook, Northamptonshire ; juveniles from the 'Middle Lias' (Quarry) at Stonehouse, Gloucestershire ; Chipping Norton, Oxfordshire ; Litchborough, Northamptonshire.

Cardinia idalia d'Orbigny 1850

Plate 4, fig. 3

1842 *Unio crassissimus* Sowerby ; Stutchbury : 483, pl. 9, fig. 7 (non Sowerby).
1850 *Cardinia idalia* d'Orbigny : 235 (Prodrome no. 169).
1907 *Cardinia idalia* d'Orbigny ; Thevinin : 44, pl. 12, figs 10–12.

MATERIAL. Several examples in the B.M.(N.H.), including the specimen here figured. Dimensions of figured specimen, LL 31270 : height 67 mm ; length 81 mm ; inflation 46 mm ; $h/l = 83{\cdot}0\%$.

Description. D'Orbigny's species is from the 'Liassien' (Pliensbachian) of France. The British specimens occur in the Marlstone of Gretton, Gloucestershire, and are virtually identical with Thevinin's (1907) figures although larger. The species is trigonal in outline but with a posterior carina demarcating a siphonal area. The dorsum is straight with a sharp change of direction where the posterior carina meets the posteroventral edge. The venter merges with the anterior in a continuous concave curve which changes to a convex curve beneath the incurled and prosogyrous umbones. The flanks have a tendency to flatness suggesting the concave condition seen in *C. slatteri* (*Nidarica* Cox) from a higher horizon.

Comparisons. *C. idalia* differs from *C. crassissima* in its more trigonal outline and the bluntly angled posterior surface ; the last character distinguishes it, together with its greater size, from the earlier *C. listeri* which it otherwise resembles.

Horizon and Locality : Marlstone, Spinatum Zone, Domerian Substage of Gretton, Gloucestershire.

Cardinia slatteri Wilson & Crick 1889

Plate 5, figs 8–10

1889 *Cardinia slatteri* Wilson & Crick : 337, pl. 10, figs 1, 2.
1961 *Nidarica slatteri* (Wilson & Crick) Cox : 335, pl. 14, figs 11–13.

Material. The lectotype, O.U.M. J 14707, selected by Cox (1961), is in the Oxford University Museum together with several other examples. Dimensions of lectotype : height 25 mm ; length 28 mm ; inflation ca. 10 mm ; $h/l = 89\%$ (Pl. 5, fig. 8).

Description. 'Opis-like, with strongly prosogyrous, terminal umbones, from which [two] prominent, angular carinae, both strongly curved with a posteriorly facing convexity, pass to the extremities of the concave ventral margin. Lunule deep, angular ; nymphs not quite so deeply sunk as in [other] *Cardinia*. No distinct cardinal teeth, but in the left valve the lunular marginal region projects and is much thickened, this projection being received in a corresponding recess in the right valve' (Cox 1961 : 335). The lateral area between the two carinae is strongly concave and the surface ornament consists of well-separated growth halts.

Comparisons. Resembling *C. idalia* but smaller, beaks more prosogyrous, and unique in having a concave lateral depression between the carinae. But some specimens of *C. idalia* from the Marlstone show a tendency towards lateral flattening, which may be antecedent to the concave condition in the later *C. slatteri*.

Discussion. Cox proposed the name *Nidarica* as a monospecific genus closely related to *Cardinia*. It is the opinion of the present writer that the hinge differs in no significant way from that of *Cardinia*, and that the presence of lateral concavities in the valves does not signify a generic distinction.

Horizon and Localities. Cox recorded the species from the Transition Bed and also from the Marlstone, but it seems to me that records from the Marlstone simply reflect a lack of differentiation in the collecting of earlier workers. Matrices examined by the present writer are all closely similar to typical Transition Bed lithology.

Transition Bed, Tenuicostatum Zone in Whitbian Substage. Aston-le-Walls and Appletree, Northamptonshire ; Tilton, Leicestershire.

Cardinia crassiuscula (J. Sowerby 1817)

Plate 2, figs 7–10

1817 *Unio crassiusculus* J. Sowerby : 191, pl. 185.
1829 *Pullastra* sp. Phillips : 161, 192.
1835 *Pullastra prototypa* Phillips : 133, pl. 13, fig. 16.
1835 *Pullastra antiqua* Phillips : 184, pl. 13, fig. 16.
1842 *Pachyodon crassiusculus* (Sowerby) Stutchbury : 483, pl. 9, fig. 8.
1849 *Cardinia crassiuscula* (Sowerby) Brown : 214, pl. 74, fig. 18.
1875 *Cardinia crassiuscula* Stutchbury ; Phillips : 254, pl. 13, fig. 16.
1875 *Cardinia antiqua* (Phillips) Phillips : 331, pl. 13, fig. 16.
1876 *Cardinia antiqua* (Phillips) Tate & Blake : 390.

MATERIAL. B.M.(N.H.) LL 31266 here designated **neotype**, collected by the author from the Frodingham Ironstone, bed 4 of Hallam (1963), about Turneri Zone ; also left and right valves, B.M.(N.H.) LL 31267–8 here figured together with the neotype. These and many others collected from the same bed at Crosby Warren, near Scunthorpe, Lincolnshire. Dimensions of neotype : height 54 mm ; length 81 mm ; inflation 32 mm ; $h/l = 67\%$ (Pl. 2, fig. 7).

DESCRIPTION. Sowerby's original description : 'Spec. Char. Oblong-elliptical, depressed ; valves thick ; surface marked by lines of growth ; hinge strong. The surface of this shell is regularly curved, without any hollow or rising ; the beaks are sharp, a little recurved ; the lines of growth are not very prominent, except two or three of them near the edge ; the hinge is light and elegant in comparison with that of *U. crassissimus* although thick'.

This shell is the most regularly ovoid of the British species of *Cardinia*. The beaks, slightly incurled, occupy the anterior quarter of the length, and the surface is covered with widely spaced, but irregularly placed, growth halts. As Sowerby observed, the hinge is relatively slender in construction and not so massively built or strongly arched as in *C. crassissima* and *C. idalia*. It is composed of the usual obsolescent 3b, AIII and PI in the right valve, and AII and PII in the left. The hinge plate of this species, and of all the ovoids, forms a flatter arch than in *C. listeri* and the rest of the deltoids, the teeth tending to be generally smaller. The ligamental nymph is deeply sunk and situated posterior to the beaks and slightly overlaps the posterior lateral tooth.

The lunule is bounded by a rather sharp ridge and is somewhat deeply excavated in some cases, while in others it is only moderately excavated, and the anterior slopes at about 40–45 degrees in a slightly concave line to the antero-ventral edge.

COMPARISONS. Resembles *C. ovalis* in outline but the beaks are more incurled, the outline more regularly ovate, the valves more evenly inflated, and the adult shell larger than that species. It is unfortunate that the similar names *crassiuscula* and *crassissima* should have caused such confusion in the minds of workers. The two names have been applied with a careless abandon and without due regard for the shape of the shell and its stratigraphical horizon when naming specimens. *C. crassiuscula* is an ovoid resembling a large *C. ovalis* and occurring abundantly in the Frodingham Ironstone of Scunthorpe, Lincolnshire ; it occurs most abundantly in the Lower Sinemurian Stage but may range outside it. *C. crassissima* is a 'hump-backed' form, resembling a large *C. hybrida,* and more closely related to the deltoids than to the ovoids ; its prosogyrous beaks are situated on the anterior sixth of the length. It occurs sparingly in the Marlstone, Spinatum Zone, Domerian Substage of Gretton, Gloucestershire. Compare Pl. 2, fig. 7 with Pl. 4, fig. 1a.

DISCUSSION. Attempts, both by the present writer and the late Dr L. R. Cox, to trace the missing type of *C. crassiuscula* have not been successful. It was collected by the Rev. G. R. Leathes 'from the Crag at Bawdsey' (Bawdsey, 9 miles SSE of Woodbridge, Suffolk). Stutchbury (1842 : 483) doubted the locality and hinted that it may have come from the Marlstone since the Crag and Marlstone fossils are often of a similar colour. However, S. V. Wood (1859 : 32–45) listed many Jurassic fossils derived into the Red Crag ; and in the B.M.(N.H.) collections there is a badly eroded left valve of *C. crassiuscula,* 43219, labelled 'Red Crag, Bawdsey'. A comparison of this with numerous specimens, collected by the present writer, from the Frodingham Ironstone of Scunthorpe, Lincolnshire, leaves no doubt as to the identity of Sowerby's original specimens with the Scunthorpe forms and the probable truth of the Bawdsey locality cited by Sowerby. The specimen from Bawdsey in the B.M.(N.H.) is a left valve, almost replaced by limonite, very crumbly, and obviously the result of weathering of the original blue-green chamositic preservation of the Frodingham Ironstone – from which it was almost certainly derived.

Examination of the holotype of Phillips' *Pullastra prototypa* (1835 : 133, = *antiqua* on p. 184) reveals that it is the young stage of *C. crassiuscula.* Tate (1876 : 390) was therefore wrong to identify Phillips' type with the small subtrigonal deltoids from the 'Sandy Series' (Lower to Middle Lias) of the Yorkshire coast. Phillips' type, TSP 232A in the York Museum, is labelled '*Cardinia antiqua* (Phil.) Robin Hood's Bay' (Pl. 2, fig. 10). The preservation and colour indicate a Lower Liassic rather than a Middle Liassic origin, and the locality may be correct. However, it may just as probably have come from the Lower Lias at Redcar, Yorkshire, or from the Drift.

HORIZON AND LOCALITIES. Semicostatum–Obtusum Zones, Sinemurian Stage. It has been reported from : Brook Down, Hatherley, Gloucestershire ; Vale of Belvoir, Leicestershire ; Crosby Warren, Yarborough and Roxby in the Scunthorpe district of Lincolnshire ; Millington, Yorkshire. It is most abundant in the Frodingham Ironstone of Lincolnshire.

Cardinia ovalis (Stutchbury 1842)

Plate 2, figs 1–3

1842 *Pachyodon ovalis* Stutchbury : 485, pl. 10, figs 17–19.
1843 *Cardinia cyprina* Agassiz : 225, pl. 12″, figs 4–6.
1843 *Cardinia unioides* Agassiz : 225, pl. 12″, figs 7–9.

Material. Stutchbury's holotype preserved in the City Museum, Bristol, C 2149, and many examples in the B.M.(N.H.) and collected by the author. Dimensions of holotype : height 32 mm ; length 46 mm ; inflation 20 mm ; h/l = 50% (Pl. 2, fig. 1).

Description. Stutchbury's original description (1842 : 485) is : 'Shell elliptical ; anterior margin rounded, posterior margin but little attenuated ; the lunule or depression of the anterior dorsal part small and narrow ; height 1·1, length 1·7, thickness 0·6'. These small shells are regularly ovate in outline with the beaks on the anterior third of the length. The surface is covered with irregularly spaced growth halts. The posterior part tends to become elongated in some, and, in some, a slight angle is developed in the postero-dorsal outline. The hinge plate is delicately constructed and the teeth small and tubercular. In the majority the anterior is projected in a regular rounded curve but a few tend to be slightly more bluntly rounded.

Comparisons. This closely resembles *C. crassiuscula* in its regularly ovate outline but differs in its tendency to elongate posteriorly, its more projected anterior outline, its tendency to develop a slight angle on the postero-dorsal outline, its small size and its stratigraphically earlier occurrence in the Hettangian. *C. hybrida* is of a similar size but is more trigonal in outline, the beaks being more prosogyrous and the anterior shorter and more steeply sloping.

Discussion. Stutchbury claimed that this species occurs in the Lower Lias at Fretherne (Lower Sinemurian), but neither Richardson (1908) nor Henderson (1934) recorded it from that locality ; the present writer, who has also examined that section, failed to find it either. However, a fairly extensive collection exists in the B.M.(N.H.) and the localities suggest that this species is mainly concentrated in the 'Angulata Zone' of earlier authors (including the Liasicus Zone of Dean, Donovan & Howarth, 1961). I have collected it from Kilve in north Somerset and from a road section west of Evesham, Worcestershire ; at both these localities it is apparently confined to the Liasicus Zone and it is extremely abundant at Evesham. The evidence indicates that this is an essentially Hettangian species and the author's collecting shows that it is most abundant in the Liasicus Zone.

Agassiz, in describing two new species of *Cardinia* from Gloucestershire, was certainly aware of Stutchbury's 1842 paper, but nevertheless he proposed the name *C. cyprina* for Stutchbury's *C. ovalis* and the name *C. unioides* for the posteriorly elongated form. Fig. 6 shows the unionid form as a group of dots beyond the 50 mm length and below the 70% h/l ratio. The diagram indicates that '*C. unioides*' is the result of a tendency to elongate posteriorly in the largest individuals of *C. ovalis*, a trend which is paralleled by *C. attenuata* in the Lower Pliensbachian Ibex Zone, but in that species very much more strongly emphasized.

This species is perhaps the most variable of all the British species of *Cardinia*, but one which, nevertheless, presents few difficulties in identification since the essentially characteristic aspect of the form is always present, no matter how the dimensions change. A comparison of Figs 6 and 7 shows the wide range of variation (Fig. 6) of *C. ovalis* which is encountered in museum collections made up of specimens from widely differing localities and horizons, and the narrower range in a collection from one locality and a narrower stratigraphical range (Fig. 7). Some of these have the posterior margin elongated and approach, but do not reach, the attenuated form of the Lower Pliensbachian *C. attenuata* from the Ibex Zone ; some are more ovate in outline and many of these have the central part inflated with the ventral margin 'pinched-in' ; some have the postero-dorsal margin regularly curved while others have a slight angle about midway to the posterior edge. Nevertheless, in all these variations the essential appearance remains and the diagrams emphasize the continuity of all the variants within the one morphospecies.

Horizons and Localities. Liasicus zone, Hettangian Stage to ? basal Bucklandi Zone in Sinemurian Stage. It is reported from : the Liasicus zone, bed H 67, in the Blue Lias west of Lyme Regis, Dorset ; Hilmorton, Wiltshire ; Lavernock, Glamorgan ; Watchet and Kilve, north Somerset ; Stretton, Gloucestershire ; Chadbury, Fladbury, Pershore and Evesham, Worcestershire ; Alcester, Binton

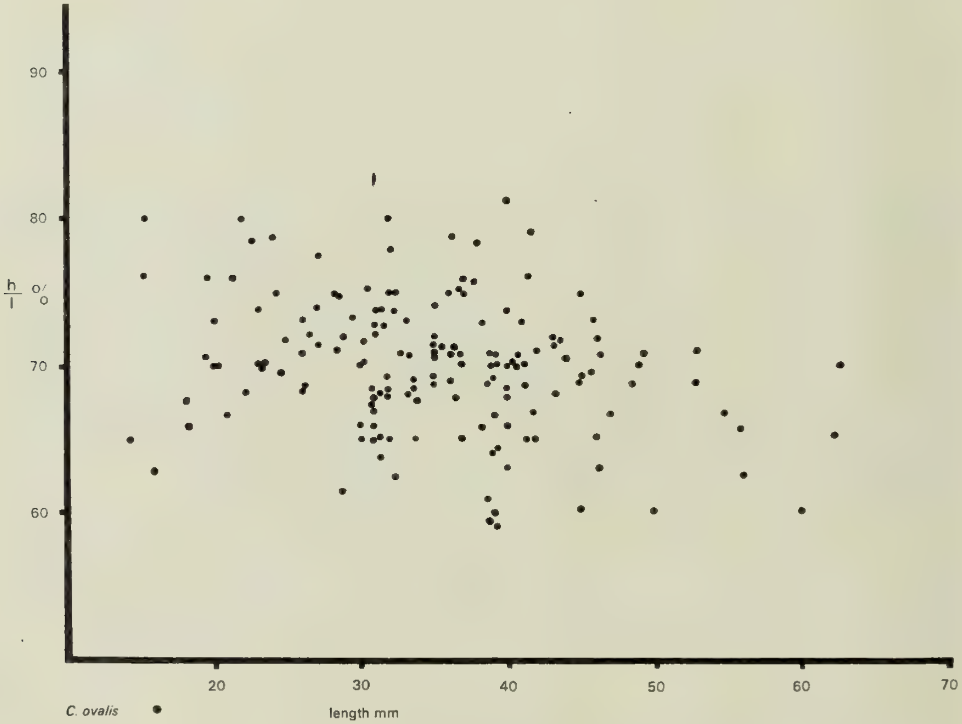

Fig. 6. All specimens of *Cardinia ovalis* in the British Museum (Natural History) were measured and plotted. They originated from various horizons in the Hettangian and their localities ranged between north Somerset and Warwickshire. The diagram demonstrates the wide morphological diversity of *C. ovalis* in large museum collections. The form *unioides* is represented by the outlying dots below and to the right. The central, upper and left-hand dots represent typical *C. ovalis*.

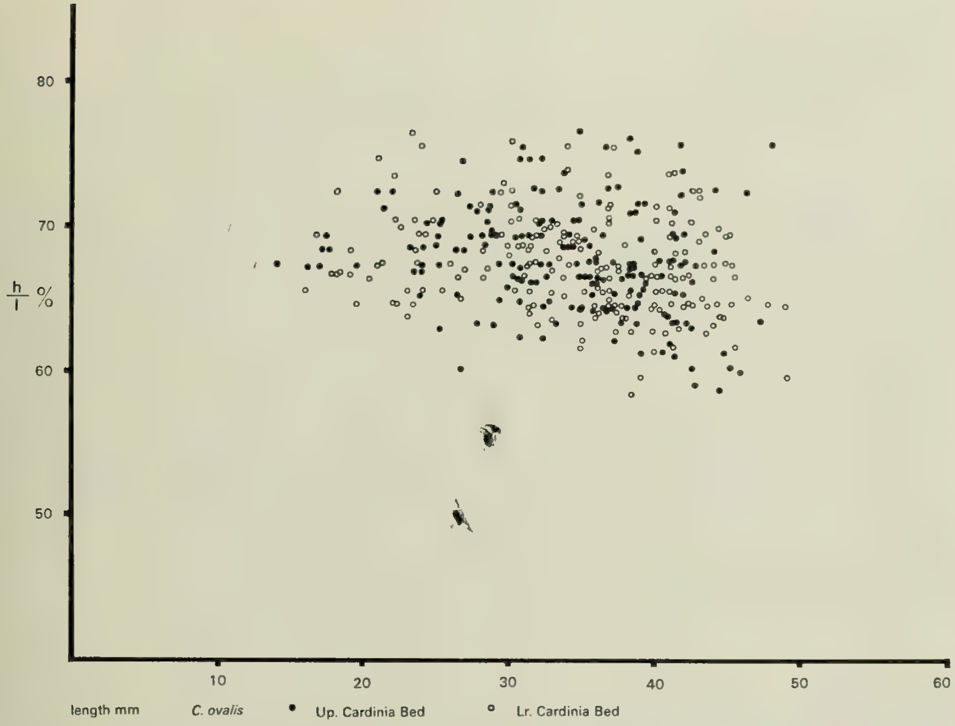

FIG. 7. In contrast with Fig. 6, a collection of *Cardinia ovalis* from one locality and horizon shows slightly reduced morphological diversity although many of the specimens suffered some degree of crushing which increased the vertical distribution on the diagram. The specimens were collected from a road cutting in the Liasicus Zone near Hampton, west of Evesham, Worcestershire. The two 'Cardinia Beds' are separated by 2–3 m of shale.

Hill and Wilmcote, Warwickshire ; Bugbrook and Kingsthorpe, Northamptonshire ; Robin Hood's Bay and Redcar, Yorkshire. Like *C. crassiuscula* in the Lower Sinemurian and *C. attenuata* in the Lower Pliensbachian, the Hettangian *C. ovalis* tends to occur very abundantly, particularly in the Liasicus Zone of Worcestershire and Warwickshire.

Cardinia huntcliffensis sp. nov.

Plate 3, fig. 8

1876 *Pullastra antiqua* Phillips ; Tate & Blake : 390.

SPECIFIC NAME. From Huntcliff on the Yorkshire Coast, see Tate & Blake (1876), figure on title page.

MATERIAL. Holotype, B.M.(N.H.) LL 23952, from the 'Margaritatus Sandstone', Margaritatus Zone, Huntcliff, Yorkshire ; also fourteen paratypes from the same horizon and locality. Dimensions of holotype: height 16 mm, length 23 mm; inflation 9 mm; $h/l = 70\%$.

DIAGNOSIS. Depressed ovoid *Cardinia* with subterminal umbones, differing from *C. hybrida* in its more prosogyrous beaks and from the young stage of *C. crassissima*, with which it might be confused, by its more ovate outline.

DESCRIPTION. Ovately cuneiform in outline, anterior short and sloping steeply to meet the slightly convex ventral edge in an even curve. The postero-dorsal outline is evenly rounded and converges towards the ventral edge which it meets at the sharply curving posterior. The surface is covered with closely spaced but irregularly placed growth halts. The lunule is small and rather shallow. The hinge is not exposed in any of the examples to hand since all are two-valved and articulated specimens. One internal mould shows two deeply set adductor muscle scars joined by an entire pallial line.

COMPARISONS. This small ovately cuneiform *Cardinia*, together with the trigonal *C. tuffleyensis*, is probably responsible for the records of *C. hybrida* ranging into the Middle Lias (Witchell 1882). It differs from *C. hybrida* in its more prosogyrous beaks and more closely spaced growth halts and its smaller lunule. From *C. tuffleyensis* it is at once distinguished by its less projecting and more steeply sloping anterior, and its more depressed outline. From the young of *C. crassissima* it differs in being more depressed and less trigonal in outline.

REMARKS. Tate (in Tate & Blake 1876: 390) identified these with Phillips' *Pullastra antiqua* (= *P. prototypa*) which, on examination of the holotype, is revealed to be the young of a *C. crassiuscula* from Robin Hood's Bay. Tate was extraordinarily confused about this species and about *C. antiqua* and *C. crassiuscula*. He says (p. 390), 'Both Strickland and Simpson are wrong in placing it under *C. crassiuscula* from which it is widely removed'. He was referring to Phillips' type which is identical with the equivalent growth stage of *C. crassiuscula* from the Lower Lias Frodingham Ironstone. He then continues to describe it: 'The shell is cuneiform, anterior side very short . . . ' etc., and clearly he was then describing the Middle Liassic Huntcliff cardiniids. It is possible that Tate, who never understood *C. crassiuscula* (cf. his pl. 14, fig. 4 with Sowerby's figure), thought that it was the name for the large Marlstone deltoids and from which *C. huntcliffensis* is certainly 'widely removed'.

HORIZON AND LOCALITIES. Domerian Substage. It is recorded from: Downcliff, Dorset, B.M.(N.H.) 67454 ex Etheridge Collection, associated with a specimen of *Pleuroceras spinatum* from the Marlstone Layer of the Junction Bed; from Chipping Norton, Oxfordshire; 0·8 km (½ mile) WNW of Upper Heyford, Northamptonshire; Huntcliff, Yorkshire.

Cardinia laevis (Young & Bird 1828)

Plate 3, figs 4–6

1828 *Cardita laevis* Young & Bird: 227, pl. 7, fig. 14.
1876 *Cardinia laevis* (Young & Bird) Tate & Blake: 391, pl. 11, fig. 12.
1961 *Cardinia laevis* (Young & Bird) Cox: 334, pl. 14, figs 3–10.

Material. The type 'has not been traced, but the specimens recorded by Tate (in Tate & Blake 1876 : 391) are in the Geological Survey Museum' (Cox 1961 : 334). The original of Cox's (1961) pl. 14, fig. 6 is here selected **neotype**. This specimen is also the original of that figured by Tate & Blake on pl. 11, fig. 12 ; IGS 7860. Dimensions : height 32 mm ; length 39 mm ; inflation 25 mm ; $h/l = 82\%$ (Pl. 3, fig. 4).

Description. 'Shell trigonal, compressed, subequilateral ; umbones acute, incurved, prominent, and approximate ; surface concentrically plicated and striated ; the striae numerous, lunule deep. Dimensions : height $1\frac{5}{12}$ inch ; breadth $1\frac{7}{12}$ inch ; thickness 1 inch' (Tate in Tate & Blake 1876 : 391). This uncommon and unusually smooth cardiniid is ovately trigonal in outline with a flat postero-dorsal margin, a broadly curved ventral edge passing into the round and projected anterior which is sharply concave beneath the incurled and prosogyrous beaks. The general appearance of this species is that of an arcticid heterodont but having the typical cardiniid hinge. The shell surface lacks the widely spaced and irregularly placed growth halts usually seen in *Cardinia*, and the young in consequence have been mistaken for *Astarte striatosulcata* (Cox 1961 : 335).

Comparisons. This species does not closely resemble any other described species of *Cardinia*. In outline it resembles *C. subabducta* but differs in its more rounded ventral and postero-dorsal outlines, and its smoother shell which develops incised growth halts only at later stages of development.

Horizon and Localities. Middle Lias Domerian Substage. It is reported from : Winterton, Lincolnshire ; Staithes, Hob Hill, Eston, and Upleatham, Yorkshire. Examination of matrices suggests that the majority of these occurrences are in the Spinatum Zone only.

Cardinia subobovata sp. nov.

Plate 4, fig. 6

Specific name. Alluding to *C. obovata* Martin 1859.

Material. Holotype, a two-valved and articulated specimen, B.M.(N.H.) L 77304, collected by J. W. Tutcher from the Angulata Zone, Maxwell Quarry, Farnborough, Somerset. No other examples have been seen. Dimensions : height 24 mm ; length 30 mm ; inflation 14 mm ; $h/l = 80\%$.

Diagnosis. Ovoid *Cardinia* resembling *C. obovata* Martin but differing from that species in its greater inflation and its more elevated and more anteriorly directed umbones.

Description. Size small for the genus, equivalve, subequilateral ; outline subobovate with the beaks situated just anterior to the mid-line, ventral margin flattened. Anterior to the beaks the outline is concave, passing into the broad curve of the anterior margin which continues in a somewhat flattened venter to a bluntly rounded postero-ventral angle where it continues, in a regularly rounded curve, to the elevated and slightly pointed beaks. The external surface of the shell, though abraded, shows about ten growth halts from the ventral margin up to 8 mm of the beak, beyond which the shell is too worn to see. The lunule is deeply impressed; the ligamental nymph, just visible in the articulated holotype, is deeply inset. Internal characters not seen.

COMPARISONS. This species closely resembles Martin's *C. obovata* from the Hettangian of the Côte d'Or in France. But it differs in its more elevated and more anteriorly placed umbones, and in its reduced inflation. Martin's figure shows a specimen with a 20 mm inflation at a height of 25 mm.

HORIZON AND LOCALITY. Hettangian, Angulata Zone at Maxwell Quarry, Farnborough, Somerset.

Cardinia suttonensis Tawney 1866

Plate 5, fig. 6

1866 *Cardinia suttonensis* Tawney: 56, pl. 4, fig. 3.

MATERIAL. Holotype in Institute of Geological Sciences, London, 7863. Specimen not well enough preserved for measurement.

DESCRIPTION. Tawney described it as being 'nearest in form to *C. regularis* Terquem, but the posterior is more acute than that species, larger and thicker. It is less cuneiform than *C. acuminata* Martin which it resembles'.

DISCUSSION. A comparison of the holotype (Plate 5, fig. 6) with Tawney's figure (1866: pl. 4, fig. 3) reveals that the figure is inaccurate and, in part, fanciful. He has restored the whole of the unexposed postero-dorsal outline and then made false comparisons with well-established forms of Terquem and Martin. Clearly the holotype, as it stands, allows neither description nor comparisons to be made and, like *C. ingens*, this form must remain, for the present, in abeyance as a *nomen dubium*.

HORIZON AND LOCALITY. Sutton Series, Hettangian; at Sutton Quarries, Glamorgan, south Wales.

Cardinia concinna (J. Sowerby 1819)

Plate 3, figs 1, 2

1819 *Unio concinnus* J. Sowerby: 43, pl. 223, figs 1, 2.
1842 *Pachyodon concinnus* (Sowerby) Stutchbury: 485, pl. 10, figs 15, 16.
1849 *Cardinia concinna* (Sowerby) Brown: 213, pl. 74, fig. 4.
1849 *Cardinia scutula* Brown: 213, pl. 88, fig. 15.

MATERIAL. Holotype, B.M.(N.H.) 43218, a single left valve, probably from the Transition Bed, Cropredy near Banbury, Oxfordshire, and many others in B.M. (N.H.). Dimensions of holotype: height 43 mm; length 79 mm; inflation 25 mm; $h/l = 54\%$ (Pl. 3, fig. 1).

DESCRIPTION. 'Spec. Char. Transversely oblong-ovate, depressed, nearly smooth, thick; posterior side very small; beaks prominent, recurved. Almost three times as wide as long, regularly convex, with a gently curved back; the thickness of the shell is remarkable ; the lines of growth are sharp ; in other respects the surface is smooth. The front is slightly incurved near the anterior end' (Sowerby 1819 : 43). Note that where Sowerby wrote 'posterior side very small' he meant 'anterior side'.

The elongated ovate outline is broken by the slightly concave anterior margin beneath the incurled beaks, which are situated at the anterior sixth of the length. The hinge plate is similar to that of *C. crassiuscula*, but altogether larger and more solid, and the usual cardiniid dentition is present. The type is from the Transition Bed, but forms from the Marlstone below tend to be larger and more rounded ventrally although otherwise indistinguishable from the true *C. concinna* at the same growth stage. Sowerby said that it was collected by Conybeare from the Inferior Oolite of Cropredy near Banbury. Conybeare obviously mistook the Marlstone outlier in the Cherwell Valley, upon which Cropredy stands, for Inferior Oolite. He may be forgiven for this since L. Richardson (1906 : 368) admits that he nearly made the same mistake at Evercreech, Somerset.

COMPARISONS. Tate placed *C. lanceolata* Stutchbury in synonymy with this species, a position which cannot be upheld here since *C. lanceolata* is from the Lower Sinemurian of Yorkshire and similar to *C. gigantea*, while the present species is from the Upper Domerian and lowermost Whitbian Substage, and is morphologically distinct. It differs from *C. gigantea* in being taller, less acute anteriorly, more rounded in the postero-dorsal outline, and not having the upswept postero-ventral margin of *C. gigantea*.

REMARKS. On the inside of the holotype, a left valve, a mass of matrix still adheres which differs considerably from the writer's experience of Marlstone matrix. It was compared with matrices of shells known to have been collected from the Transition Bed (Tenuicostatum Zone) of the Midlands. The buff-coloured, finely oolitic matrices were very similar, and it is suggested that Sowerby's type came from the Transition Bed – Upper Lias, Whitbian Substage. The type of *C. scutula* Brown is a typical Marlstone form which Brown wished to distinguish from the smaller Transition Bed forms, since he believed, on the evidence of Conybeare, that Sowerby's type came from the Inferior Oolite.

HORIZON AND LOCALITIES. Marlstone, Spinatum Zone and Transition Bed, Tenuicostatum Zone ; Domerian to Whitbian Substages. It is reported from South Petherton and Ilminster, Somerset ; Stonehouse and Tuffley, Gloucestershire ; Adderbury and Cropredy, Oxfordshire ; Staverton, Northamptonshire ; Vale of Belvoir, Leicestershire ; Denton, Lincolnshire ; Staithes and Cleveland, Yorkshire.

Cardinia gigantea (Quenstedt 1856)

Plate 3, fig. 3

1856 *Thalassites giganteus* Quenstedt : 81, pl. 10, fig. 1.

MATERIAL. Several examples in the B.M.(N.H.) including the specimen here figured on Pl. 3, fig. 3. Dimensions of figured specimen : height 51 mm ; length 120 mm ; inflation 34 mm ; $h/l = 42{\cdot}5\%$.

Description. Concinnoid *Cardinia* with a more inflated shell, due to its relatively reduced height, than the taller and more flat-sided *C. concinna*. The flat postero-dorsal margin is almost parallel with the longitudinal axis and meets the evenly rounded, and posteriorly upswept, ventral margin in a tight curve. The anterior is more acutely rounded and slopes at a low angle and in a straight line from the small and depressed umbones. The lunule is fairly deeply excavated and the beaks slightly incurled. The shell surface is covered with irregular growth halts.

Comparisons. The upswept posterior of this species gives the shell a flattened and horizontal postero-dorsal outline and this, together with the small and pointedly projected anterior, distinguishes it from the round-backed, round-fronted, taller *C. concinna*.

Remarks. Quenstedt's original figured specimen came from the Lower Sinemurian of Gmuend, Germany. He recorded it from the Lower Lias in beds just below the occurrence of *Caenisites turneri* and above that of *Agassiceras scipionianum*. Concinnoids occur in Britain most commonly in the condensed Liassic deposits around the Radstock area in Somerset (usually only as internal moulds), in the Frodingham Ironstone of Lincolnshire, and in the Marlstone and Transition Bed. Those from Radstock and Frodingham are of Sinemurian age and stratigraphically earlier than those from the Marlstone and Transition Bed. Since these concinnoids are similar in shape, confusion by earlier authors has resulted in the apparent range of the stratigraphically higher *C. concinna* being extended down to include the specimens from the Sinemurian localities. The latter, being morphologically distinct, are therefore best assigned to Quenstedt's *C. gigantea* and the higher Domerian–Whitbian forms to Sowerby's *C. concinna*.

Horizon and Localities. Semicostatum–Obtusum Zones, Lower Sinemurian. Radstock, Somerset ; Scunthorpe, Lincolnshire ; Redcar, Yorkshire.

Cardinia lanceolata (Stutchbury 1842)

Plate 2, fig. 4

1842 *Pachyodon lanceolata* Stutchbury : 484 (text-figure).
1849 *Cardinia lanceolata* (Stutchbury) Brown : 213, pl. 88, figs 18, 19.

Material. Stutchbury's holotype, B.M.(N.H.) 47578, ex Bean Collection from the Lower Lias of Robin Hood's Bay, Yorkshire ; no other material seen. Dimensions : height 37 mm ; length 88 mm ; inflation 25 mm ; $h/l = 44\%$.

Description. Stutchbury described it 'shell lanceolate, anterior portion $\frac{1}{6}$ of the length, posterior portion acutely produced ; hinge line straight ; height 0·7, length 1·2, thickness 0·4'. This sole specimen has a straight postero-ventral margin which meets the evenly rounded venter in an acutely rounded posterior curve. The anterior is less sharply curved, passing into a shallow concavity in the anterior outline at the lightly excavated lunule. The moderately incurled beaks are situated on the anterior seventh of the length. A bluntly rounded umbonal ridge runs from the umbo to the sharply curved posterior, and the surfaces of the valves are covered with irregular growth halts. The ventral edges of the valves are remarkably thickened and channelled, presenting the 'carinate–bisulcate' appearance of an arietitid ammonite. The hinge, not seen in the two-valved and articulated holotype, is probably similar to that of *C. gigantea*.

Both Stutchbury and Brown have depicted the shell as too short, and Agassiz has figured *C. attenuata* (1842–5 : pl. 12″, figs 1–3) under the name '*C. lanceolata*'.

COMPARISONS. *C. lanceolata* is similar to both *C. gigantea* and *C. attenuata* ; from the first it differs in being more sharply attenuated posteriorly, and from the second in being more bluntly acuminate anteriorly. *C. concinna* from the Domerian resembles this species but is more ovate in outline and not nearly so obviously 'pointed' posteriorly.

DISCUSSION. Tate (in Tate & Blake 1876 : 389–390) mistakenly placed this species in synonymy with *C. concinna* and recorded both from the Bucklandi Zone (in Tate's sense this includes the Bucklandi–Turneri Zones of Dean, Donovan & Howarth 1961). Henderson (1934 : 550) recorded it from the Semicostatum Zone of Fretherne, Gloucestershire.

HORIZON AND LOCALITIES. Lower Sinemurian. Fretherne, Gloucestershire ; Robin Hood's Bay, Yorkshire.

Cardinia attenuata (Stutchbury 1842)

Plate 2, figs 5, 6

1842 *Pachyodon attenuatus* Stutchbury : pl. 10, figs 13, 14.
1843 *Cardinia lanceolata* (Stutchbury) Agassiz 224, pl. 12″, figs 1–3 (non Stutchbury).
1849 *Cardinia attenuata* (Stutchbury) Brown : 213, pl. 88, fig. 20.
1904 *Cardinia attenuata* (Stutchbury) Richardson : 220, pl. 15, fig. 10.

MATERIAL. Holotype in City Museum, Bristol, C 2156, and many others in that museum and also in the B.M.(N.H.). Dimensions of figured specimen, L 7020 : height 34 mm ; length 74 mm ; inflation 15 mm ; $h/l = 46\%$ (Pl. 2, fig. 6).

DESCRIPTION. 'Shell cuneiform ; transverse diameter twice its height ; posterior end strongly attenuated ; lunule small but deep ; transverse diameter 2·8, height 1·4, thickness 0·7' (Stutchbury 1842 : 485). The shell is ovately cuneiform with the dorsal and ventral margins converging posteriorly from the broadly rounded anterior, which terminates at a small lunule beneath slightly incurled and approximated beaks. The shell looks as if a typically elongated *C. ovalis* had become further 'stretched' out in a posterior direction so that the length is more than twice the height. The anterior has a broadly rounded curve, like a typical *C. ovalis*, which contrasts with the narrowly rounded posterior. The beaks are placed on the anterior quarter to fifth of the length, and are small and slightly projected. The hinge is lightly constructed, with small teeth as in *C. ovalis* and the rugoid group. Some examples are more cuneiform than others from the same bed owing to a relative reduction in the length. In the Raricostatum–Oxynotum Zones of Yorkshire and Raasay in Scotland an attenuated cardiniid occurs which is closely comparable in outline with the shortest examples of this species. These fall within the range of variation of the

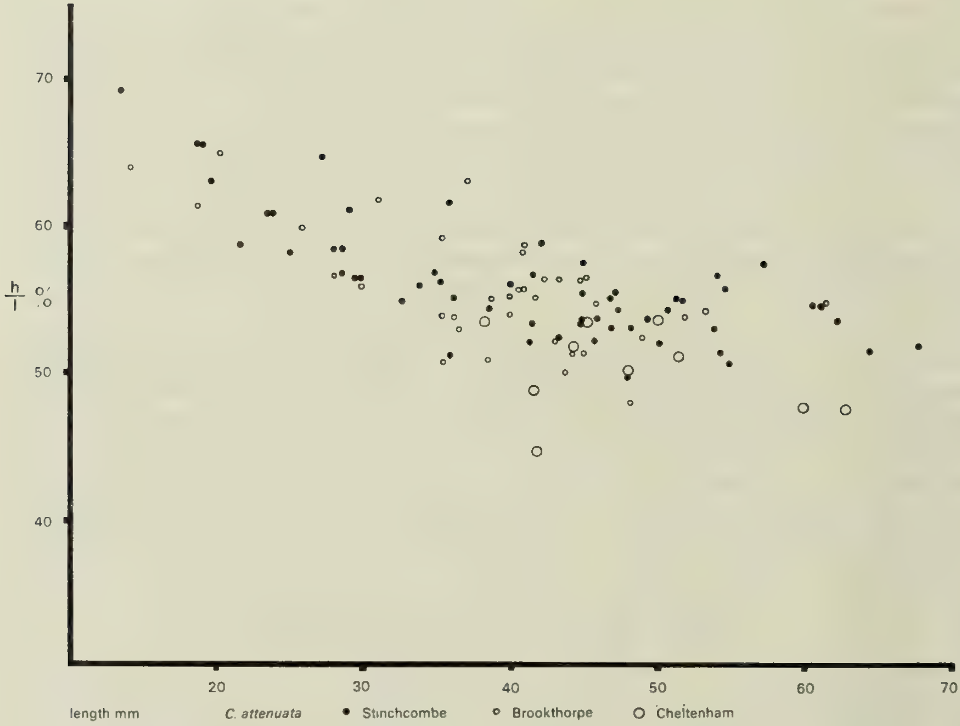

FIG. 8. *Cardinia attenuata* collected by Dr M. K. L. Curtis and Mr T. Fry from three localities in the Ibex Zone of Gloucestershire. The diagram demonstrates the reduction of the height : length ratio with increase in size.

stratigraphically higher Ibex Zone specimens of *C. attenuata* and are therefore here accepted as being conspecific.

COMPARISONS. Anterior to the beaks this is almost indistinguishable from the Hettangian *C. ovalis*, but the posterior portion is more extended and attenuated. It cannot be confused with *C. hybrida* since the beaks, as in *C. ovalis*, are set further back from the anterior margin. The anterior is more broadly rounded than in any of the other members of the concinnoid group.

REMARKS. Agassiz was misled by Stutchbury's poor sketch of *C. lanceolata* (1842 : 484) into believing that it was the same as *C. attenuata*. His figure of *C. lanceolata* (pl. 12″, figs 1–3) is based on a specimen from the Lias of Cheltenham, Gloucestershire, and there is no doubt that he has drawn a typical *C. attenuata*. A large collection of this species was made at several localities in the Ibex Zone of Gloucestershire. Fig. 8 shows the distribution of the height : length ratios and clearly demonstrates the increase of length with growth.

HORIZON AND LOCALITIES. Raricostatum Zone, Upper Sinemurian to Ibex Zone, Carixian Substage. It is reported from Cheltenham, Leckhampton, Battledown, Mickleton, Stow Hill, Cam, Dumbleton, Stinchcombe, Brookthorpe, all in Gloucestershire; Blockley clay pit, Worcestershire; Napton and Little Wolford, Warwickshire; Kilsby Tunnel and Kingsthorpe Shaft, Northamptonshire; Husbands Bosworth, Leicestershire; Robin Hood's Bay, Yorkshire; Pabba Shales of Raasay, Scotland.

Cardinia tuffleyensis sp. nov.

Plate 4, figs 4–5

1882 *Cardinia hybrida* (Sowerby) Witchell: 107, pl. 2, fig. 4.

Specific name. From the village of Tuffley on the southern flanks of Robin's Wood Hill in Gloucestershire.

Material. Holotype a right valve only, B.M.(N.H.) LL 31275, from the Middle Lias, Margaritatus Zone, Bed 14, Tuffley, Robin's Wood Hill, Gloucestershire. Paratypes: one left valve from the same bed and locality as the holotype, and four single valves from the equivalent horizon, bed 10, at Stonehouse, Gloucestershire. Dimensions of holotype: height 31·2 mm; length 74·4 mm; inflation 8·0 mm; $h/l = 58\%$ (Pl. 4, fig. 4).

Diagnosis. Concinnoid *Cardinia* resembling the young stages of the Marlstone forms of *C. concinna* but differing in its greater height : length ratio and flatter dorsal outline.

Description. Size small for a concinnoid *Cardinia*, ovately trigonal in outline, inequilateral, beaks situated at the anterior quarter of the length, inflation slight. Beaks pointed, prosogyrous, overhanging a deeply impressed lunule which, in the holotype, is bounded by a sharp ridge – paratypes do not exhibit this ridge. The anterior outline is slightly concave beneath the umbones and meets the regularly curving ventral margin in a bluntly rounded anterior projection. The distinct umbonal ridge descends steeply, nearly parallel with the dorsal margin, to the posterior edge, and growth lines and growth halts change direction sharply as they pass over the umbonal ridge. In the interior, the regular, but asymmetrical, arch of the hinge plate is interrupted by a ventrally directed fold at the posterior end of the deeply sunken nymph, and is terminated abruptly by the deeply set anterior and posterior adductor muscle scars. The left valve has the usual anterior socket and long posterior lateral. The right valve has an anterior peg-like lateral tooth and a long posterior socket.

Comparisons. This species closely resembles the equivalent growth stage of the much bigger, and stratigraphically higher, *C. concinna*, but it differs in its greater height : length ratio giving the shell a much taller appearance. Comparative h/l percentage ratios for the two species are: *C. concinna*, from the Marlstone, Spinatum Zone, 52%, 50%, 49%; *C. tuffleyensis*, from the Margaritatus Zone, holotype 58%, paratypes 62%, 60%, 59%.

Horizon and Localities. Margaritatus Zone of the Domerian Substage. Bed 10 at Stonehouse Brick and Tile Co. Clay Pit, Gloucestershire; Bed 14 at Tuffley Clay Pit, Robin's Wood Hill, Gloucestershire (Palmer 1972).

Cardinia rugulosa Tate 1875

Plate 5, fig. 5

1875 *Cardinia rugulosa* Tate : 508, text-fig. 3.

MATERIAL. Tate's original, which came from the Jamesoni Zone of Mungar quarry, Paulton, Somerset, cannot be traced in the Institute of Geological Sciences. However, B.M.(N.H.) L 77306, from the '*armatus* Zone' (Jamesoni Zone) of Bince's Lodge near Radstock, Somerset, is similar to Tate's sketch although slightly more sharply angled in its postero-dorsal outline. This specimen, a right valve, is here figured on Plate 5, fig. 5. No other material has been seen. Dimensions of figured B.M.(N.H.) specimen : height 9·5 mm ; length 15 mm ; inflation about 5 mm ; $h/l = 63{\cdot}5\%$.

DESCRIPTION. The sole specimen, a right valve, is small (15 mm long), and subquadrate in outline with the umbones on the anterior quarter of the length. The dorsal and ventral margins are nearly parallel, while the posterior slopes steeply from the sharp angle in the postero-dorsal margin. The beaks are small, and slightly incurled above a moderately excavated lunule. The surface is covered with about nine imbricating lamellae with upturned edges. The hinge, but poorly seen, is apparently similar to that of *C. ovalis* and *C. dayi*. Tate (1875 : 508) remarked of his specimen that the surface was 'ornamented with thick folds of growth, the umbonal ones with erect lamellose edges', and leaves no doubt that he was describing the same form as that figured here on Plate 5, fig. 5.

COMPARISONS. *C. rugulosa* is similar to *C. dayi* and *C. tutcheri*, and also to *C. toriyamai* Hayami (1958) from Japan, but it differs from all these in its squarer outline and more sharply angled postero-dorsal margin. This, together with its stratigraphically earlier occurrence, requires that it be treated as a distinct species.

HORIZON AND LOCALITY. Jamesoni Zone, Carixian Substage of the Radstock area, Somerset.

Cardinia dayi sp. nov.

Plate 5, fig. 3

SPECIFIC NAME. After E. C. H. Day, who first described the Shell Bed in the Middle Lias of the Dorset Coast from which the type material was collected.

MATERIAL. Holotype, a left valve only, B.M.(N.H.) LL 31271. Paratypes : one right valve, B.M.(N.H.) LL 31272, and two left valves, LL 31273–4. All from Day's Shell Bed in the Middle Lias of the Dorset Coast ; all are broken. Dimensions of holotype : height 18·5 mm ; length 27·5 mm ; estimated inflation 9 mm ; $h/l = 65{\cdot}5\%$.

DIAGNOSIS. Rugoid *Cardinia* resembling *C. torayamai* Hayami but differing from that species in its flatter ventral margin, more ovate outline and more deeply excavated lunule. From *C. rugulosa* it differs in its greater size and more ovate posterior outline.

Description. Size small for the genus, ovate, inequilateral, the beaks at about the anterior quarter of the length, inflation slight. Beaks slightly undercut at the antero-dorsal margin and strongly prosogyrous. Anterior margin (broken in holotype) sloping steeply from the subumbonal undercut and passing into a strong anterior curve which grades into the slightly convex outline of the ventral margin. A sharp curve at the postero-ventral margin passes into the smooth convexity of the postero-ventral outline, which is terminated at the anteriorly pointing beaks. Lunule small and bounded by a bluntly rounded ridge.

The exterior of the holotype has about fourteen concentric, flat, stepped lamellae which are slightly turned up at the edges and covered by fine growth lines. In the interior the slightly asymmetrical, but regularly arched, outline of the hinge plate is broken by a faint ventrally directed convexity below the nymph. The hinge plate is terminated at either end by the slightly impressed adductor muscle scars. Pallial line entire.

In the hinge the usual obsolescent cardinal 3b can barely be made out in the right valve, and the arrangement of the lateral teeth is typically cardiniid. The anterior part of the left valve contains a deep depression in the hinge plate for the reception of the peg-like protuberance at the end of the single anterior lateral tooth in the right valve. The posterior laterals of the right valve are formed by the dorsal margin (behind the nymph) beneath which a hollow is formed by a tooth which arches down from the hinge plate just behind the nymph, curves sharply, and rises to meet the hinge plate again just above the posterior adductor scar. The ventral outline of the hinge plate above this tooth is not altered by its presence and maintains a regular arching curve. A single posterior lateral in the left valve fits into the socket thus formed.

Horizon and Locality. Lower Jurassic, Domerian, Margaritatus Zone Stokesi Subzone, Bed 20 of Howarth (1958), 'Day's Shell Bed', Seatown to Eype, Dorset coast.

Cardinia tutcheri sp. nov.

Plate 5, figs 1–2

Specific name. After J. W. Tutcher who collected the holotype.

Material. Holotype, B.M.(N.H.) 77369, a left valve from the Marlstone layer of the Junction Bed, Spinatum Zone, Thorncombe Beacon, Dorset ; J. W. Tutcher Collection. Paratype, B.M.(N.H.) 67374, a right valve only, which is badly eroded in the umbonal region, from the Middle Lias of Chideock, Dorset ; Etheridge Collection. In the paratype, the hard crystalline matrix enclosing ferruginous ooliths is identical with that of the holotype, so it also certainly came from the Marlstone layer (Spinatum Zone) of the Junction Bed. Dimensions of holotype : height 28·5 mm ; length 50·5 mm ; inflation 8 mm ; $h/l = 57\%$ (Pl. 5, fig. 1).

Diagnosis. Rugoid *Cardinia* resembling *C. dayi* but differing in its reduced height : length ratio and more incurled beaks.

Description. Medium size (length of largest specimen, the paratype, is 56 mm), elongate and ovate in outline, inequilateral, beaks at about the anterior quarter of the length, inflation moderate.

Comparisons. This species strongly resembles *C. dayi* in all respects except in its greater relative length, slightly less prosogyrous beaks, and flatter ventral margin. The shell surface is composed of strongly imbricating flat lamellae upon which are fine growth lines. The hinge of neither specimen has been examined owing to the difficulty of developing the relatively soft shells from the hard crystalline matrix, but there are no reasons for supposing that the hinge differs much from that of *C. dayi* and *C. toriyamai*. However, the greater length of the shell implies that the hinge plate may be expected to form a flatter arch.

Horizon and Localities. Lower Jurassic, Domerian, Spinatum Zone, Marlstone layer of the Junction Bed. Seatown to Eype, Dorset coast.

V. EVOLUTION AND PALAEOECOLOGY

Evolution. Few exact statements may be made in this section because the establishment of a correct sequence of forms of *Cardinia* is entirely dependent on accurate zonal data accompanying the material to be studied. Unfortunately, this information is nearly always absent, even in the large accumulations of fossil bivalves constituting national collections. The stratigraphical assignments in Section IV are largely based on the author's field experience and deductions made from the literature. The former, though believed to be reliable, is always insufficient for our needs, while the latter, though abundant, is not always reliable. However, given that the horizons are more or less correct, the following tentative picture emerges.

The earliest British Jurassic forms are those occurring in the Hettangian Sutton Series of south Wales (a peculiar lithology consisting of white limestone with angular fragments of rock derived from the Carboniferous Limestone), a deltoid, *C. ingens*, and an ovoid, *C. suttonensis*. *C. ingens* has been seen in Liassic marginal facies around the Mendips and in Wurt Pit near East Harptree where it is associated with the ammonite *Psiloceras*. This deltoid is a strong candidate for the ancestor of *C. listeri* and *C. hybrida*, but no more so than the continental *C. angustiplexa* Chapuis & Dewalque or *C. dunkeri* Chapuis & Dewalque, both from the Hettangian Marne de Jamoigne of eastern France. However, the deltoids in Britain appear to have had a straightforward development through *C. listeri/hybrida* (Bucklandi–Semicostatum Zones), *C. raasayi* (Raricostatum Zone) to *C. idalia* (Spinatum Zone), and very probably to *C. slatteri* (Tenuicostatum Zone) since *C. idalia* is already, in the Spinatum Zone, developing a strong posterior carina and concave sides.

The ovoids probably developed from the doubtful *C. suttonensis* (Planorbis zone) to *C. ovalis* (Liasicus–Angulata Zones) and *C. crassiuscula* (Semicostatum–Obtusum Zones). It seems probable that *C. attenuata*, though grouped with the concinnoids on general shape, developed from one of the ovoids, rather than one of the concinnoids or one of the deltoids such as *C. hybrida*, since the ovoids have a rounded anterior margin and a tendency to elongate posteriorly (cf. *C. ovalis* var. *unioides*, p. 21) whereas *C. hybrida* has more prosogyrous beaks over a steeply sloping anterior.

The origin of the concinnoids is obscure but it seems probable that they evolved from one of the ovoid stock. Having done so somewhere in the Sinemurian they subsequently maintained themselves as a tight group from *C. lanceolata* (Bucklandi–Turneri Zones), to *C. gigantea* (Semicostatum–Obtusum Zones) and *C. concinna* (Margaritatus–Tenuicostatum Zones).

In the rugoids it is easier to demonstrate a stratigraphical sequence because there are fewer examples, and these are from well-documented horizons ; the trends shown by them seem to be straightforward. A specimen of *Cardinia* sp. in the B.M.(N.H.) (66216, purchased from M. Tesson in 1896 ; Pl. 5, fig. 4) is recorded from the 'Upper Lias' of France. No other information is available, but the French origin is not in doubt since it is registered next to one lot of *C. gibbosula* d'Orbigny (= *C. itea* d'Orbigny) from the 'Upper Lias of Fontaine Etoupefour, France', the preservation of which is identical with that of specimen no. 66216. The surface sculpture and shape closely resemble those of *C. tutcheri* from the Marlstone of Dorset but it is more depressed and, in this character, it continues the trend seen in the earlier rugoids, and provides a terminal form to an interesting stratigraphical sequence. This starts with the small square *C. rugulosa* and is continued with the larger and more ovate *C. dayi* which, by depression of the dorsal margin and elongation, leads to *C. tutcheri* and finally to the un-named French form exemplified by B.M.(N.H.) 66216.

The height : length ratios of these forms, at 15 mm height, are as follows :

Species	Horizon	Locality	*h*/*l* (%)
Cardinia sp.	Toarcian	France	50
C. tutcheri	Spinatum Zone	Dorset	57
C. dayi	Margaritatus Zone	Dorset	66
C. rugulosa	Jamesoni Zone	Somerset	63·5

No difference in the character of the hinge is detectable between the earliest and latest cardiniids. The functional anterior and posterior laterals remain constant both in position and size and, apart from slight individual variations, they do not alter. The sole obsolescent cardinal tooth 3b in the right valve can usually be detected as a more or less elongated rounded ridge. Examination of a number of hinges shows a tendency for this tooth to be most strongly developed in deltoids, and weakest in ovoids, but it is never sufficiently developed to be regarded as functional.

Beyond the Transition Bed (Tenuicostatum Zone) there are no reliable records of *Cardinia* in Britain and it seems, from the available evidence, that the genus became extinct at this horizon in Britain and later, during Whitbian times, throughout Europe.

PALAEOECOLOGY. Cardiniids are found in almost every kind of Liassic lithology ; shales, limestones, sandstones, ferruginous oolitic limestones but not in paper shales. It does not seem possible to relate any of the infrageneric groups to a particular lithology, except that the author has not seen a concinnoid from a shale or muddy deposit.

The associates of *Cardinia* are many, varied and almost always molluscs ; and of these, considered singly, only *Astarte* has been found to be a frequent associate. At

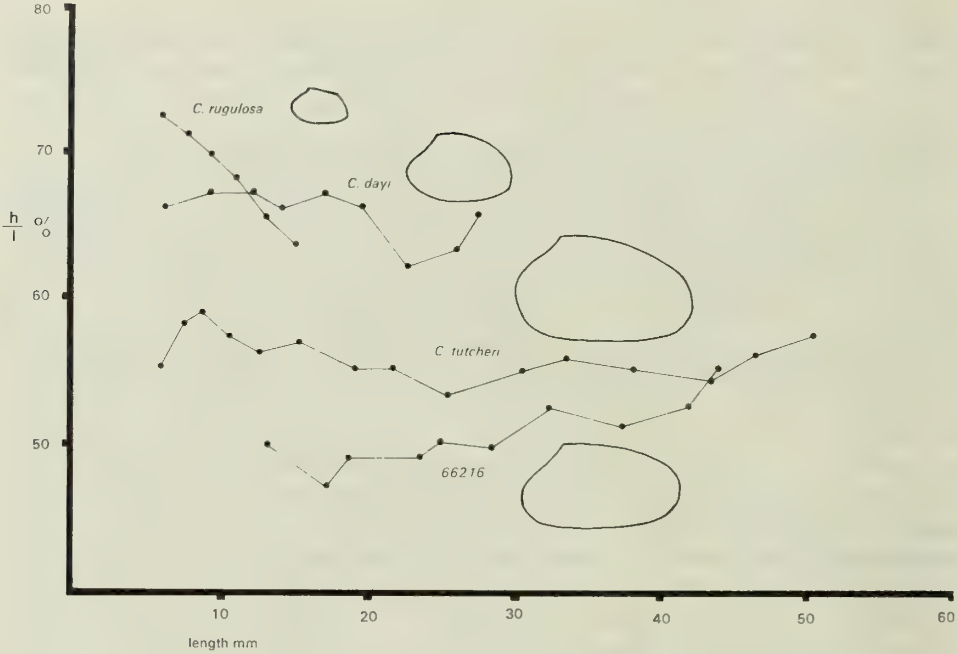

Fig. 9. A stratigraphical sequence of British rugoid cardiniids ; oldest at the top, youngest at bottom. The diagram represent height : length ratios in *Cardinia rugulosa*, Jamesoni Zone ; *C. dayi*, Margaritatus Zone ; *C. tutcheri*, Spinatum Zone ; and the French specimen, B.M.(N.H.) 66216, from the Whitbian Substage at Fontaine Etoupefour. The tendency towards elongation in the development of *C. rugulosa*, and also in the sequence of *C. dayi*, *C. tutcheri* and specimen 66216, is well demonstrated by this diagram. The possibility that this might in fact be an evolutionary sequence cannot be overlooked. Measurements were made on single valves of each of the species at various growth stages and outlines drawn as left valves for uniformity.

Kilve in north Somerset *C. ovalis* is found in Hettangian shales and is there accompanied by *Astarte obsoleta* Dunker, in the proportion of 10–15 *Cardinia* to 1 *Astarte*. The only other associates, apart from ammonites, are rare oysters and even rarer scaphopods. The same two species are also found in Hettangian shales at Evesham, Worcestershire, where the ratio is about 15–20 *Cardinia* to 1 *Astarte*, but there the association is masked by the presence of other bivalve molluscs, particularly *Liostrea irregularis* (Münster). At a higher horizon in the Frodingham Ironstone of Lincolnshire, *Cardinia* and *Astarte* also occur together, but there the *Astarte* is rare, and the estimated ratio is about 50–100 *Cardinia* to 1 *Astarte*.

The richly fossiliferous shell beds seen at Blockley, Worcestershire, and around Cheltenham and Gloucester, Gloucestershire, are in the Ibex Zone. In Gloucestershire both *Astarte* and *C. attenuata* are abundant in the Valdani Subzone, but in the slightly later (Luridum Subzone) shell bed at Blockley Station *Astarte platymorpha* Cossman (Palmer 1973 : 260) dominates to the exclusion of *C. attenuata* which does, however, occur in the clays below, somewhat rarely and without *Astarte*. This apparent 'trend' is negated in the Margaritatus Zone of Gloucestershire and Dorsetshire, for there the two are again associated. In Gloucestershire they are about equally rare, and in Dorsetshire *Astarte* dominates about 15 : 1.

It is difficult to offer convincing reasons why these two genera should exhibit such an erratic relationship, and one is tempted to speculate on possible physio-chemical factors of the benthonic environment, and isostatic movements of the seafloor, when possibly the relative abundance of the two genera was controlled simply by the distribution of their larvae in the plankton. The ecological factor which controlled the absolute distribution of *Cardinia*, that is whether they are present or not, is no easier to discover, for clearly sediment grade played little or no part. The hypothesis that they were controlled by the availability of dissolved oxygen is a little devious and admittedly tenuous, but it is perhaps worth expounding.

Of the many factors controlling the distribution of bivalve molluscs the essential three are a suitable substrate for the settlement of spat, and the availability of food and dissolved oxygen. In *Cardinia* the shell-shape and absence of a pallial sinus indicate that they were shallow burrowers ; while the strong shear-resistant lateral teeth forming the hinge indicate that they were also active animals. Active, shallow-burrowing, filter-feeding bivalves need suspended organic debris, and oxygen to 'drive' the filtering gill.

Cardiniids are often associated, among other things, with small holostomatous gastropods belonging to the Trochacae. It has already been shown that the presence of trochid gastropods has some depth implications (Palmer 1973 : 261), since almost all living trochids are algal grazers and are therefore necessarily confined to the 'photic zone' which, for the purpose of this argument, is best extended down to its lowest limit of about 100 m. The two *Cardinia* beds in the Frodingham Ironstone contain an ovoid *C. crassiuscula* and a concinnoid *C. gigantea* in the ratio of 10–20 to 1. Their abundance in the ironstone contrasts with their virtual absence from the shales above which, at Roxby, extends to the Upper Lias. The inhibiting factor is not easy to discover since ovoids are present, and abundant, in the shales at Evesham but there they are associated with a small trochid gastropod in the lower of the two *Cardinia* beds. In the shales above this bed both the *Cardinia* and the trochid are absent, or so rare as to have escaped the attention of three careful searchers ; the *Cardinia* does not return until the Upper *Cardinia* bed, some 6 m higher in the succession, where it is accompanied by abundant oysters and *Modiolus* but apparently without the gastropod.

The presence of the trochids in the silty sediments of the Lower *Cardinia* bed at Evesham strongly suggests that it was deposited within 100 m depth, and their absence from the finer shales above suggests a depth below 100 m. Deepening of the water below 100 m may have deprived the algal-grazing trochids of their food, but not the filter-feeding cardiniids since the presence of *Plagiostoma* in the shales above the Lower *Cardinia* bed proves that food was available. The evidence at Kilve and Blockley shows that fine shales are a suitable substrate for the settlement of *Cardinia* spat. It is therefore concluded that oxygen availability was the controlling factor in the distribution of *Cardinia* in the Hettangian shales at Evesham and very probably wherever it occurs. Deepening of the Liassic sea, as indicated by a change to finer sediments, could not by itself have affected the distribution of *Cardinia*. Only when this was accompanied by a significant drop in the dissolved oxygen content were the active, filter-feeding *Cardinia* unable to feed – even when food was available.

The life position of *Cardinia* may be tentatively inferred from the following observations. Two B.M.(N.H.) specimens show borings of other organisms (? sponges) along the postero-dorsal margin. The first is the holotype of *C. concinna*, see Pl. 3, figs 1, 2 ; the second is B.M.(N.H.) 43219, the *C. crassiuscula* derived into the Red Crag (p. 20). The borings are shallow circular holes occupying such a position as to indicate that the shells lay partially buried in sediment with their long axes inclined up to about 60 degrees from the horizontal, and possibly with the posterior part of the shell just protruding above the surface of the sediment. But since the majority of cardiniids show no signs of boring or encrusting organisms it seems probable that they were for the most part entirely buried in the sediment while alive. Only occasionally were dead shells exposed as a result of erosion, and these, which were almost certainly in the life position if undisturbed by bioturbation, were then available for boring organisms to attack.

VI. GENERIC RELATIONS

The taxonomic history of *Cardinia* was thoroughly reviewed by Cox (1961) and for the present purposes the following summary will suffice. In 1817 J. Sowerby described four new fossil shells which he named *crassissimus*, *listeri*, *hybridus* and *crassiusculus* ; he referred these shells with confidence to the fresh-water genus *Unio* and in doing so remarked with some astonishment that Mr Parkinson '– has, not without doubting, made it a *Donax*'. The subsequent recognition that these typically Liassic shells constituted a distinct genus from *Unio* resulted in the rapid proposal of the names *Thalassides* Berger 1833, *Ginorga* Gray 1840 (nom. nud.), *Cardinia* Agassiz 1841, *Sinemuria* de Christol 1841, *Pachyodon* Stutchbury 1842, and much later *Storthodon* Zittel 1881. Opinion 292 (1954) of the International Commission on Zoological Nomenclature validated the name *Cardinia* dating from Agassiz 1841 with *Unio listeri* J. Sowerby as type species, and suppressed *Thalassides* Berger and *Sinemuria* de Christol. Hayami (1958 : 21) unfortunately cited *Unio concinnus* as type species after the publication of Opinion 292 in which *Unio listeri* J. Sowerby was declared the type species.

The history of the systematic positioning of the genus is one which reflects the confusion resulting from a shell with the superficial appearance of a unionid but with an undoubted heterodont hinge. Agassiz (1843) placed it near the Unionidae, while Woodward (1854) placed it near the 'Cyprinidae' (i.e. Arcticidae). Chenu (1862) thought it was a crassatellid, while Stoliczka (1871) placed it in the Astartidae. Zittel (1881 : 61) proposed the family Cardiniidae which included not only *Cardinia* but several non-heterodont genera which are now referred to the Anthracosiidae and Pachycardiidae. Fischer (1887) placed Zittel's family Cardiniidae just before the Carditidae and only two families subsequent to the Unionidae – a fine compromise. Subsequent authors, who included Neumayr, Waagen, Dall, Deschaseaux and Cox, expressed opinions that oscillated between relating the Cardiniidae either to the Unionidae or to one of the two heterodont families Astartidae and 'Cyprinidae' (Arcticidae). The present position of the genus, and a more rationally composed family Cardiniidae, in the *Treatise on Invertebrate Paleontology* (Cox 1969 : N578) is in the Crassatellacae next to the Crassatellidae. While supporting the inclusion of the Cardiniidae in the Heterodonta its position in the Crassatellacae is here challenged, and arguments in support of placing the genus *Cardinia* and the family Cardiniidae in the Lucinacae are offered below.

Cox (1961 : 328) remarked that 'forms with cardiniid dentition show a very similar range in external morphology to forms with astartid dentition'. He continued by citing three examples :

(1) the Triassic genus *Torastarte*, originally referred by its author Marwick (1953 : 70) to the Astartidae, but subsequently shown to be a cardiniid by Fleming (1957) ;
(2) the young of *Cardinia laevis*, frequently misidentified and recorded as *Astarte striatosulcata* Roemer ;
(3) the close similarity of the remarkable *Cardinia slatteri* Wilson & Crick to the astartid genus *Opis*.

These are strong arguments in support of his position and he might have continued to show the parallel development in shape of *Cardinia concinna* (J. Sowerby) and *Coelastarte excavata* (J. Sowerby) ; of *Cardinia listeri* (J. Sowerby) and the astartid *Bythiamena isosceles* Gardner ; of *Cardinia ovalis* (Stutchbury) and *Astarte dentilabrum* Etheridge ; and of *Cardinia quadrata* Agassiz and the three rhomboid astartids *A. platymorpha* Cossmann, *A. camertonensis* Moore and *A. rhombea* Roemer. But perhaps Cox was not altogether convinced, since none knew better than he that little significance can be attached to similarities in general morphology in support of postulated relationships when, as in this case, the really significant factor, the hinge, clearly showed that cardiniids and astartids are not closely related.

The dentition of an astartid is typically composed of two strong cardinals in each valve with laterals either absent or but weakly developed. There are departures from this pattern but they are not typical. On the other hand *Cardinia* constantly has strong laterals which, unlike the astartid lamellar teeth, tend to be tubercular. The cardinals are always weak or absent and it is difficult to recognize more than the single tooth 3b in the right valve.

Two examples can now be cited that should counter Cox's citation of *Torastarte* (which looks like an astartid but has a cardiniid dentition), as evidence of astartid affinities. They also show that the relationship of *Cardinia* is more likely to be with the Lucinacae.

(1) Cossmann (1904 : 521, pl. 17, figs 28, 29) published figures of a remarkable ovoid cardiniid, from the Hettangian (Infralias) of La Vendée, France, which he called *Cardinia lucinaeformis*, and which looks like a *Lucina* but has the hinge of a *Cardinia*. This fact would have clearly no more significance than a bivalve which has the appearance of an astartid and the hinge of a cardiniid (Cox's argument) were it not for the remarkable similarity that the hinge of the small Sinemurian lucinoid

bivalve '*Lucina*' *limbata* Terquem & Piette has to that of a typical cardiniid. Pl. 5 fig. 11 demonstrates in *Lucina limbata* the obsolete *Cardinia*-like cardinal teeth and the anterior lateral AII and AIV forming a socket for the reception of AIII in the right valve. Strong posterior laterals in the left valve make a socket for the reception of the tooth PIII in the right valve. The rest of the hinge with its weak cardinal 3b and strong laterals is very similar in general appearance to the hinge of *Cardinia*.

(2) Further evidence, demonstrating a greater affinity of *Cardinia* with lucinids than with astartids, includes :

(i) The external shell surface of *Cardinia* is made up of concentric, imbricating lamellae, sometimes with upturned edges as in the rugoids *C. dayi*, *C. rugulosa*, *C. tutcheri* and *C. toriyamai*. A similar kind of shell surface is found in many lucinids, but astartids generally have concentric undulations, almost never with imbricating lamellae.

(ii) In *Cardinia* the concentric ornament during ontogeny tends to get stronger whereas in astartids there is a tendency for concentric ornament to weaken.

(iii) The margin of *Cardinia* is always smooth while astartids usually have a denticulate ventral margin to the shell.

(iv) The ligament is clearly visible and external in astartids, making a prominent arch behind the umbones. In *Cardinia* it is deeply sunk within a narrowly lanceolate escutcheon. The condition of a deeply set ligament in the Lucinacae is common.

VII. CONCLUSIONS

The genus *Cardinia* is probably more closely related to Lucinacae than to Crassatellacae and the same is very probably true of the family Cardiniidae, as now constituted. The origins of the genus remain obscure but the Triassic genus *Torastarte* with its *Cardinia*-like hinge, similar external appearance and deeply sunk ligamental nymph is an obvious candidate. The extinction in Europe of *Cardinia* in the Whitbian Substage of the Toarcian Stage seems to coincide with the widespread transgression and change of fauna and lithology at that level. Little is known of the ecology of *Cardinia* except that they were clearly active, shallow burrowers in many kinds of sediments and, since they were bigger and more numerous in high energy environments and are seldom, if ever, found in paper shales, it is suggested that availability of oxygen rather than of food was the controlling factor in their distribution.

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PLATE 1

All figures are natural size

Cardinia listeri (J. Sowerby) (p. 11)

Fig. 1. Lectotype, B.M.(N.H.) LL 31297. The original of J. Sowerby's (1817) syntype figured on pl. 154, fig. 1, from 'Durham'; exterior of left valve.

Fig. 2. Paralectotype, B.M.(N.H.) 43221. The original of J. Sowerby's figured syntype from 'Scarborough'; exterior of left valve.

Fig. 3. B.M.(N.H.) LL 31265. Evesham, Worcestershire; right valve interior.

Cardinia raasayi sp. nov. (p. 15)

Fig. 4. Holotype, B.M.(N.H.) L 76713. Raricostatum Zone, Allt Fearns, Raasay, Inverness-shire, Scotland; exterior of right valve.

Cardinia hybrida (J. Sowerby) (p. 12; see also Pl. 3, fig. 7)

Fig. 5. Holotype, B.M.(N.H.) 43222. From 'Nottinghamshire'. a, exterior of left valve; b, exterior of right valve.

Fig. 6. B.M.(N.H.) L 28721. Redmile, Lincolnshire; interior of left valve.

Cardinia hybrida, var. ***depressa*** (Zieten) (p. 12)

Fig. 7. B.M.(N.H.) L 17923. Bengworth, Worcestershire; interior of left valve.

Fig. 8. B.M.(N.H.) L 17936. Drake's Broughton, Worcestershire; exterior of left valve.

Cardinia subabducta sp. nov. (p. 14)

Fig. 9. B.M.(N.H.) L 382. Gloucestershire; exterior of right valve.

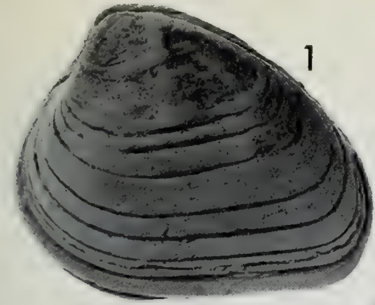
Fig. 10. Holotype, Bristol City Museum C 2158. 'Lias near Cheltenham'; exterior of right valve.

Cardinia imbricata (Stutchbury) (p. 14)

Fig. 11. Paralectotype, Bristol City Museum C 2151. Fretherne, Gloucestershire; interior of right valve.

Fig. 12. Holotype, Bristol City Museum C 2151. Fretherne, Gloucestershire; exterior of left valve.

Fig. 13. B.M.(N.H.) L 78419. Fretherne, Gloucestershire; exterior of right valve.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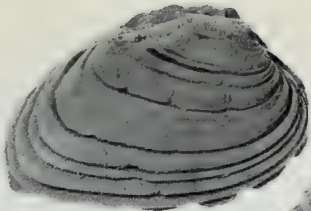

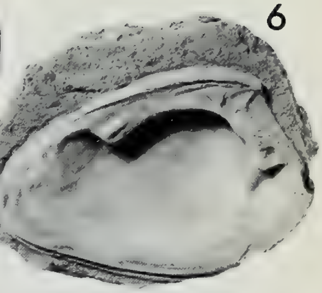
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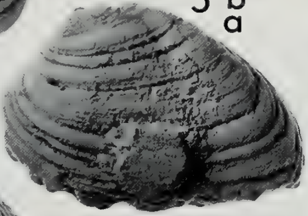

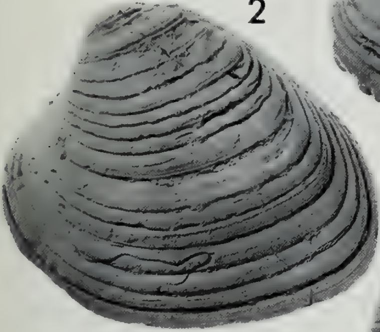
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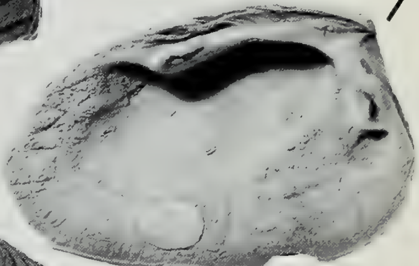
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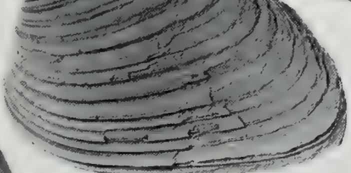
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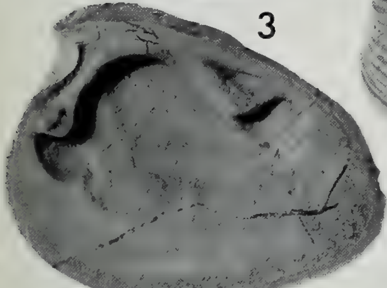
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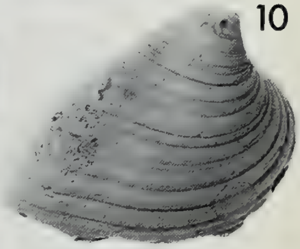
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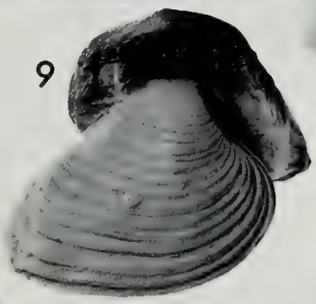
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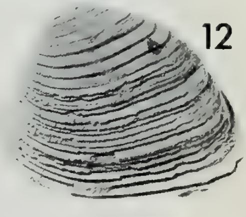
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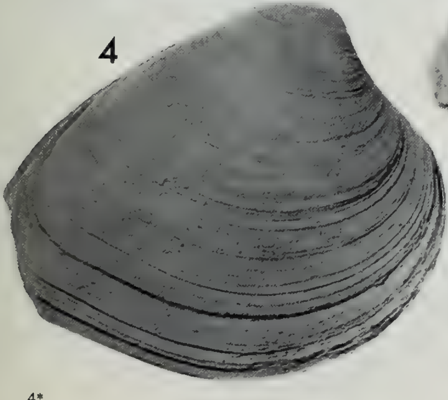
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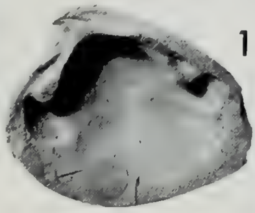
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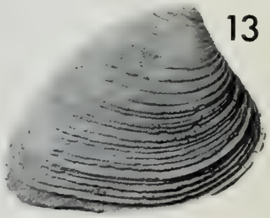
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PLATE 2

All figures are natural size

Cardinia ovalis (Stutchbury) (p. 20)

FIG. 1. Holotype, Bristol City Museum C 2149. 'Lias, Fretherne, Gloucestershire'. a, exterior of left valve ; b, exterior of right valve.

FIG. 2. B.M.(N.H.) 89012. Mickleton, Gloucestershire ; exterior of left valve.

FIG. 3. B.M.(N.H.) L 7022. Mickleton, Gloucestershire ; interior of right valve.

Cardinia lanceolata (Stutchbury) (p. 28)

FIG. 4. Holotype, B.M.(N.H.) 47578. Robin Hood's Bay, Yorkshire ; exterior of left valve. *ex* Bean Collection.

Cardinia attenuata (Stutchbury) (p. 29)

FIG. 5. Holotype, Bristol City Museum C 2156. 'Lias, Battledown, near Cheltenham' ; exterior of left valve.

FIG. 6. B.M.(N.H.) L 7020. Stow Hill, Gloucestershire ; exterior of left valve.

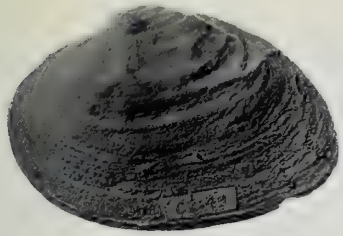
Cardinia crassiuscula (J. Sowerby) (p. 19)

FIG. 7. Neotype herein designated, B.M.(N.H.) LL 31266. Bed 4 of Hallam (1963 : 555), Frodingham Ironstone, Crosby Warren, near Scunthorpe, Lincolnshire ; exterior of left valve.

FIG. 8. B.M.(N.H.) LL 31267. Same horizon and locality as neotype ; interior of right valve.

FIG. 9. B.M.(N.H.) LL 31268. Same horizon and locality as neotype ; interior of left valve.

FIG. 10. Holotype of *Pullastra antiqua* Phillips, York Museum TSP 232A. 'Lias, Robin Hood's Bay' ; exterior of left valve.



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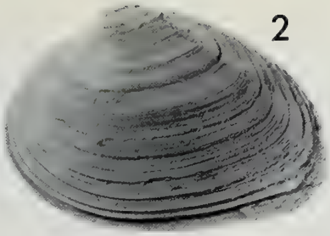

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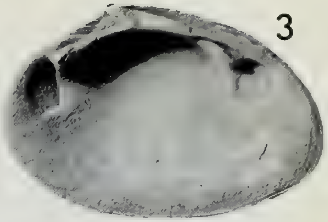

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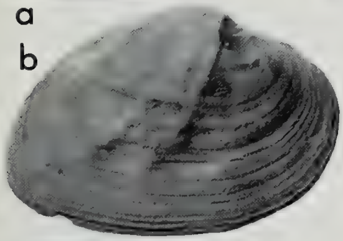

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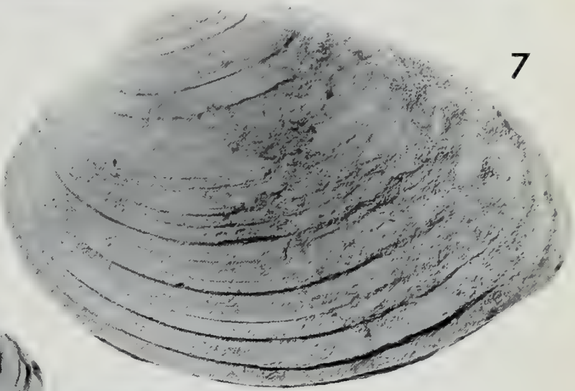

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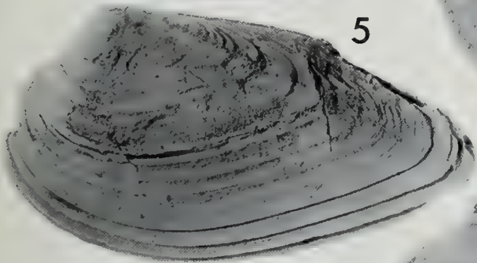

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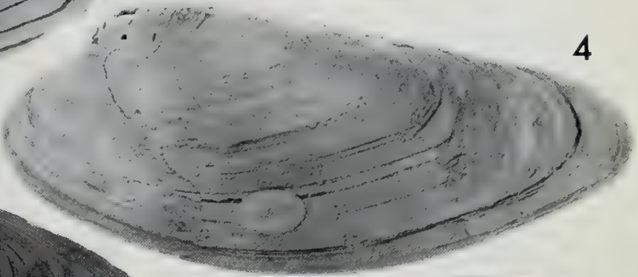

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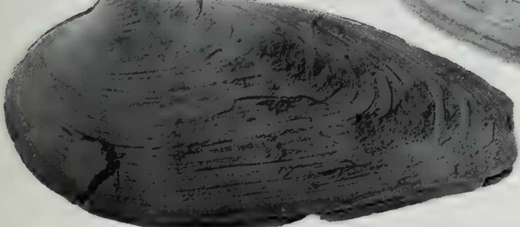

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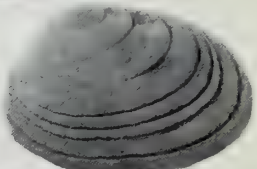

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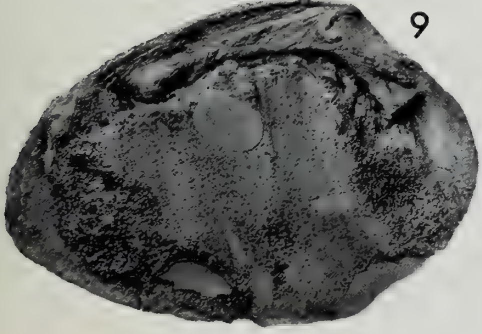

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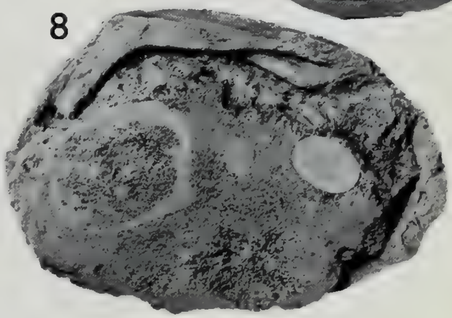


PLATE 3

All figures are natural size

Cardinia concinna (J. Sowerby) (p. 26)

Fig. 1. Holotype, B.M.(N.H.) 43218. Cropredy, Oxfordshire. a, exterior of left valve; b, interior of left valve.

Fig. 2. B.M.(N.H.) L 18469. Domerian, Spinatum Zone, Cleveland, Yorkshire; exterior of left valve.

Cardinia gigantea (Quenstedt) (p. 27)

Fig. 3. B.M.(N.H.) LL 31269. 'Fordsham' – ? Fordham, Cambridgeshire or ? Frodingham, Lincolnshire; exterior of right valve.

Cardinia laevis (Young & Bird) (p. 24)

Fig. 4. Neotype herein designated, IGS 7860, original of Tate 1876 : pl. 11, fig. 12. Domerian, Spinatum Zone, Eston, Yorkshire; exterior of right valve. (Cox 1961 : pl. 14, fig. 6)

Fig. 5. IGS 7858, original of Tate 1876 : pl. 11, fig. 7 (as *Astarte striato-sulcata*). Domerian, Spinatum Zone, ? Eston, Yorkshire; exterior of left valve. (Cox 1961 : pl. 14, fig. 7).

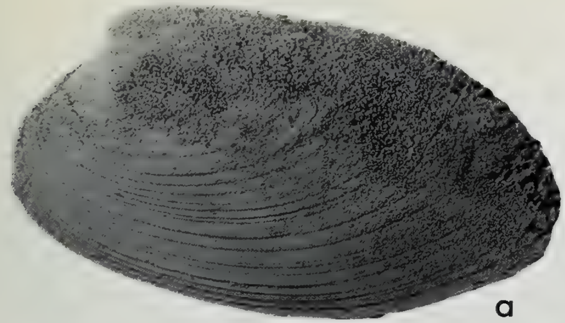
Fig. 6. IGS 31460. Domerian, Spinatum Zone, Hobb Hill, Yorkshire; exterior of right valve. (Cox 1961 : pl. 14, fig. 4).

Cardinia hybrida (J. Sowerby) (p. 12; see also Pl. 1, figs. 5–8)

Fig. 7. Holotype of *C. cuneata* (Stutchbury), Bristol City Museum C 2154. 'Lias, Fretherne, Gloucestershire'; exterior of left valve.

Cardinia huntcliffensis sp. nov. (p. 23)

Fig. 8. Holotype, B.M.(N.H.) LL 23952. Sandy Series, Margaritatus Zone, Huntcliff, Yorkshire; exterior of left valve.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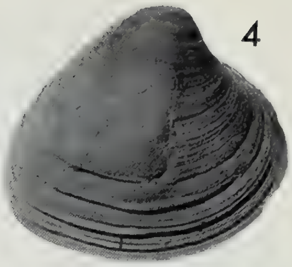
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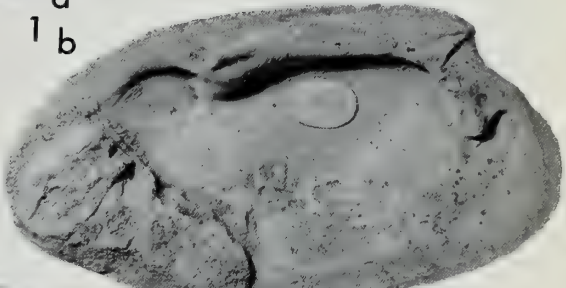
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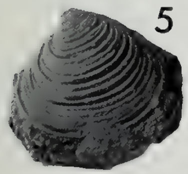
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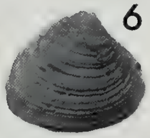
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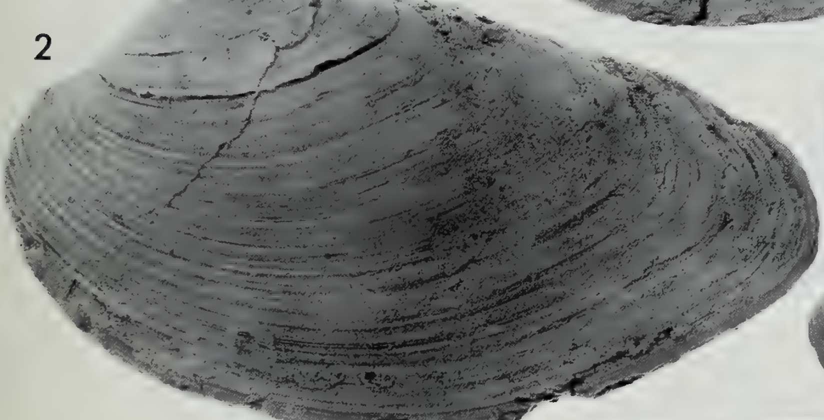
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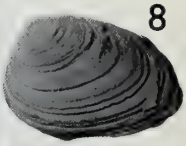
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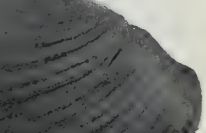
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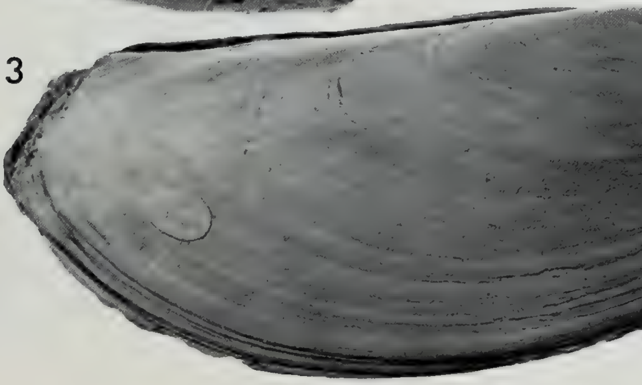
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PLATE 4

All figures are natural size, except Fig. 3

Cardinia crassissima (J. Sowerby) (p. 16)

FIG. 1. Holotype, B.M.(N.H.) 43219, the original of Sowerby's (1817) pl. 153. 'Marlstone of Tail's Hill, Gloucestershire'. a, exterior of left valve ; b, interior of left valve.

FIG. 2. B.M.(N.H.) 67210, a juvenile silicified cast. Domerian of Dumbleton Hill, Gloucestershire ; interior of right valve. The lenticular anterior adductor scar, in contrast with the orbicular posterior adductor scar, seems constant for the species : cf. Fig. 1b. above.

Cardinia idalia d'Orbigny (p. 17)

FIG. 3. B.M.(N.H.) LL 31270. Marlstone of Gretton, Gloucestershire ; exterior of right valve. × ½.

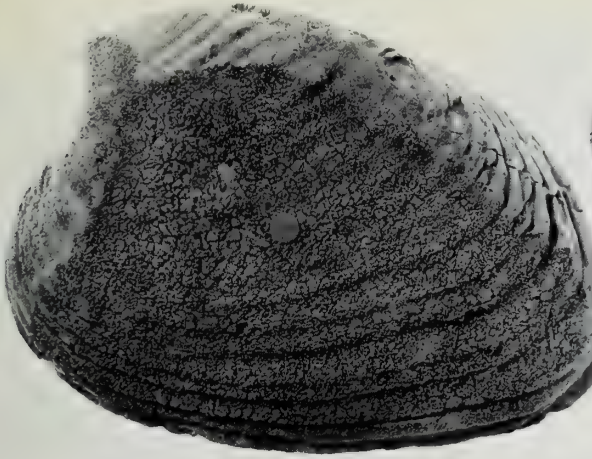
Cardinia tuffleyensis sp. nov. (p. 31)

FIG. 4. Holotype, B.M.(N.H.) LL 31275. Bed 14, Subnodosus Subzone, Margaritatus Zone, Tuffley Clay Pit, Robin's Wood Hill, Gloucestershire. a, exterior of right valve ; b, interior of right valve.

FIG. 5. Paratype, B.M.(N.H.) LL 31276. Same locality and horizon. a, exterior of left valve ; b, interior of left valve.

Cardinia subobovata sp. nov. (p. 25)

FIG. 6. Holotype, B.M.(N.H.) L 7304. Hettangian, Angulata Zone, Maxwell Quarry, Farnborough, Somerset ; exterior of left valve.



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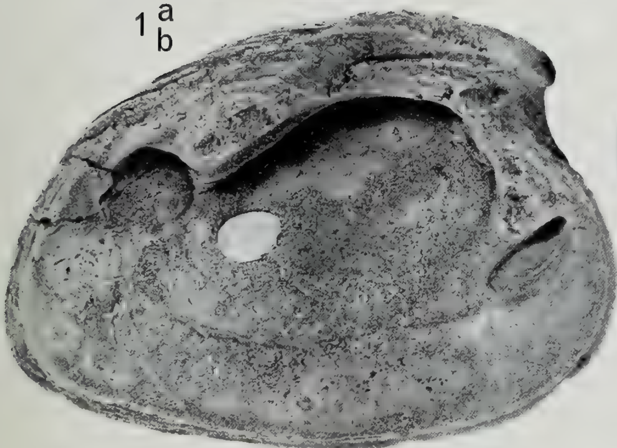

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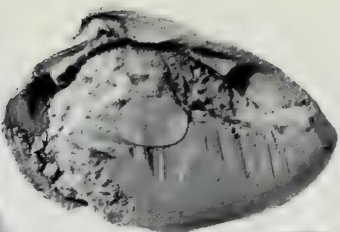

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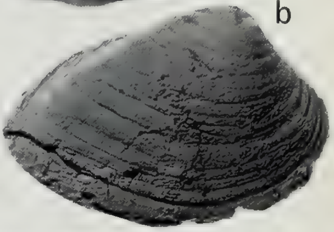

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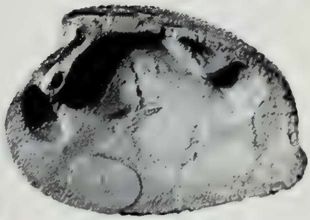

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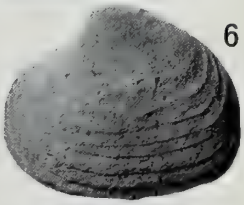

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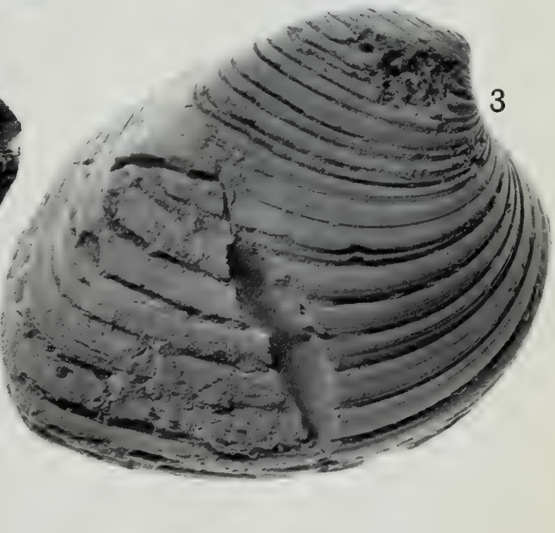

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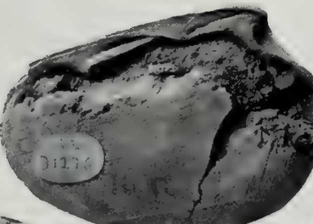

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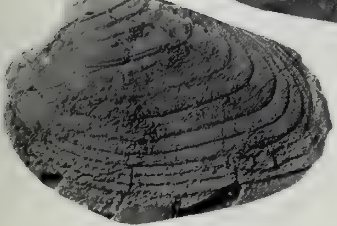


a

PLATE 5

Cardinia tutcheri sp. nov. (p. 33)

FIG. 1. Holotype, B.M.(N.H.) 67374. Bed 34, Marlstone layer of Junction Bed, Spinatum Zone, 'Chideock', Dorset; exterior of right valve. *ex* R. Etheridge Collection. × 1.

FIG. 2. Paratype, B.M.(N.H.) L 77369. Same horizon, Thorncombe Beacon, Dorset; exterior of left valve. × 1.

Cardinia dayi sp. nov. (p. 32)

FIG. 3. Holotype, B.M.(N.H.) LL 31271. Bed 20, 'Day's Shell Bed', Stokesi Subzone, Margaritatus Zone, 400 yards (366 metres) east of Seatown on Ridge Cliff, Dorset. a, exterior of left valve; b, interior of left valve. Both × 2.

Cardinia sp. (p. 35)

FIG. 4. B.M.(N.H.) 66126. Upper Lias, Fontaine, Etoupefour, France; exterior of left valve. × 1.

Cardinia rugulosa Tate (p. 32)

FIG. 5. B.M.(N.H.) L 77306. Carixian, Jamesoni Zone, Binces Lodge near Radstock, Somerset; exterior of right valve. × 2.

Cardinia suttonensis Tawney (p. 26)

FIG. 6. Holotype, IGS 7863. Lower Lias, Sutton Stone, Sutton, Glamorgan; exterior of left valve. × 1.

Cardinia ingens Tawney (p. 16)

FIG. 7. Holotype, IGS 91989. Lower Lias, Sutton Stone, Brocastle, Glamorgan; internal mould of right valve. × $\frac{1}{2}$.

Cardinia slatteri Wilson & Crick (p. 18)

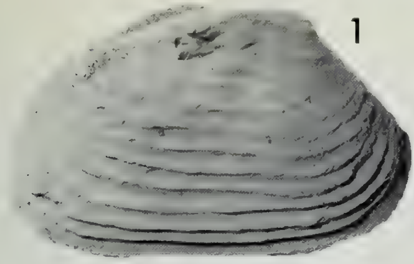
FIG. 8. Lectotype, OUM J 14707. Tenuicostatum Zone, Transition Bed, near Aston-le-Walls, Northamptonshire. a, exterior of right valve; b, interior of right valve. Both × 1. (Cox 1961 : pl. 14, fig. 11b, a).

FIG. 9. OUM J 14708. Same horizon, Appletree, near Aston-le-Walls, Northamptonshire. a, interior of left valve; b, exterior of left valve. Both × 1. (Cox 1961 : pl. 14, fig. 13a, b).

FIG. 10. OUM J 14706. Horizon and locality as last; exterior of right valve. × 1. (Cox 1961 : pl. 14, fig. 12).

Lucina limbata Terquem & Piette (p. 40)

FIG. 11. B.M.(N.H.) L 11389. c. Bucklandi Zone, Bengeworth, near Evesham, Worcestershire; interior of left valve showing *Cardinia*-like hinge. × 2.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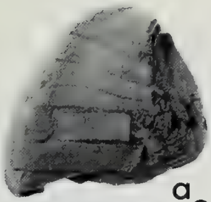
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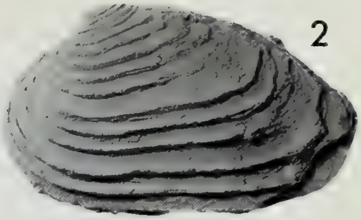
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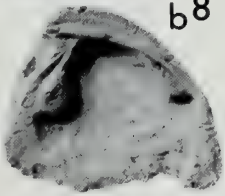
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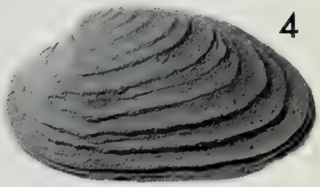
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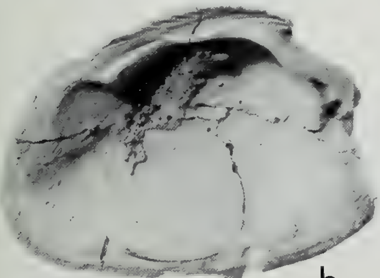
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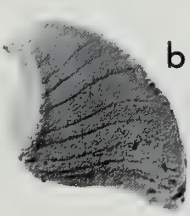
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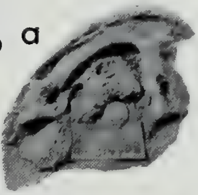
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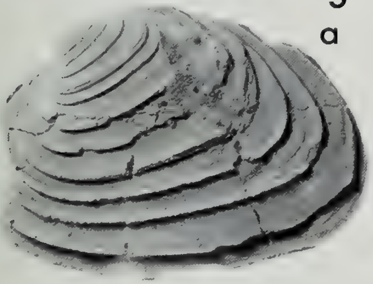
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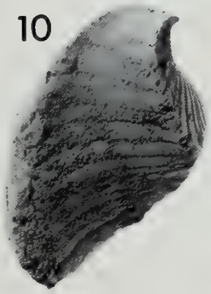
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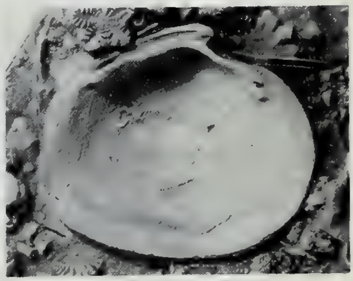
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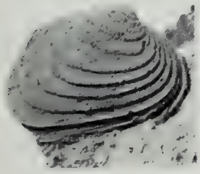
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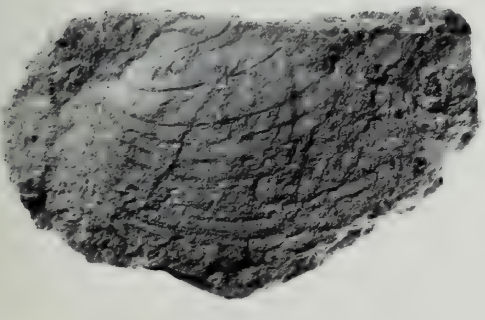
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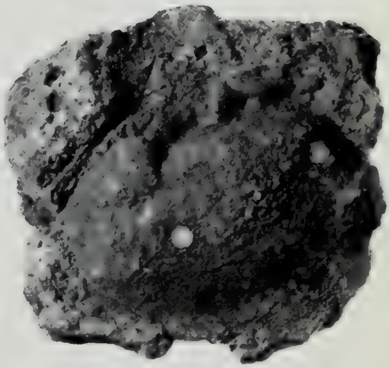
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THE SHELL STRUCTURE OF THE LIASSIC AMMONITE FAMILY DACTYLIOCERATIDAE

M. K. HOWARTH

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 26 No. 2
LONDON: 1975

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BY

MICHAEL KINGSLEY HOWARTH

Pp. 45–67 ; 10 *Plates* ; 2 *Text-figures*

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By MICHAEL KINGSLEY HOWARTH

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ABSTRACT

Dactylioceratidae are thought to be unique amongst Jurassic and Cretaceous ammonites, in that, as well as the normal main shell with its thin Outer Prismatic, thick Nacreous and thin Inner Prismatic Layers, they also possess an inner shell, consisting of thin Outer Prismatic and thick Inner Nacreous Layers, which is added to the inside of the main shell, but bridges across the inside of the ribs leaving cavities with characteristic flat floors. The inner shell lines the whole of the lateral and ventral parts of the main shell, while its front edge is $\frac{1}{8}$ to $\frac{1}{2}$ whorl behind the mouth border and is similar in shape. It is formed by division of the Inner Prismatic Layer when ventral ribs first develop three whorls after the protoconch. At the rear of the body chamber another new layer, the thick Septal Prismatic Layer, lines the whole of the inside of the shell, including the dorsum, where it bridges across the ribs of the venter of the previous whorl leaving crescent-shaped cavities. Septa are a direct development of that layer, which is present on the dorsum from the mouth of the protoconch, and spreads to line the whole of the shell when the ribs first develop.

The main purpose of the inner shell was probably to smooth the inside of the body chamber to allow easier movement prior to the formation of each septum. The Triassic family Trachyceratidae also possesses an inner shell that is probably similar. The nearest comparable structures in Jurassic and Cretaceous ammonites are dorsal shields, and floors to spines and keels.

I. INTRODUCTION

Close examination of any well-preserved ammonite of the family Dactylioceratidae reveals the presence of two shells on at least the last three whorls up to the adult aperture. The main shell overlies a second inner shell of similar thickness and development. In almost all cases the inner shell does not follow the form of the inner surface of the main shell exactly, but cuts across the inside of the ribs to leave flat-floored rib cavities. The resulting flat tops to the ribs of the inner shell are easily seen without the aid of a hand lens or microscope. When the ammonites are preserved in calcareous nodules, the main shell usually adheres strongly to the outer matrix of the nodule, while the inner shell adheres to the matrix or cast inside the ammonite, so the nodule splits along the junction between the main and inner shells of the ammonite. The outer matrix is then frequently discarded by collectors, and the ammonite that is retained consists of the inner shell only, with characteristic flat-topped ribs.

These features of Dactylioceratidae were first recorded by Buckman (1909 : ix, x), who proposed the terms 'septicosta' and 'septicostate' to describe the hollow ribs cut off by a septum on the inside; he also pointed out that this was a good character by which to distinguish them from homeomorphic Bathonian and later Perisphinctidae which do not have septicostate ribs. No further comment appeared until Guex (1970) described the phenomenon again, and gave photographs and drawings showing the extent of the inner shell in some Bifrons Zone Dactylioceratidae. The macroscopic features of the main and inner shells in species of *Dactylioceras* from the Tenuicostatum Zone in the Upper Lias of Yorkshire were described by Howarth (1973 : 249–252), who included cross-section drawings through the shell structure, and many illustrations in the plates of the different appearances of the inner and outer surfaces of the main and inner shells.

Although the presence of both main and inner shell can be seen in any well-preserved Dactylioceratidae, details of the structures of individual layers have been obscured by recrystallization in all but a few exceptional cases. Thus all the Dactylioceratidae from many different horizons in the Upper Lias of the Yorkshire coast have recrystallized shells in which the original aragonite is not preserved. Only the main features of the main shell and the inner shell as single entities can be seen. They are of interest, however, at horizons where pyrites replacement has occurred, for it is apparent that the main and inner shells behave as independent layers even when they are in close contact, as in the interspaces.* Complete replacement of the inner shell by pyrites sometimes occurs where the attached main shell consists of recrystallized calcite. The junction between the recrystallization and the pyrites replacement corresponds exactly with the junction between the main and inner shells. This independent behaviour of the two shells can only be explained in terms of the layers of which each consists : the thin layer of prismatic crystals (the Inner Prismatic Layer) that occurs between the two must have acted as a barrier to the pyritic replacement that occurred from the inside and prevented it from reaching the main shell.

---

* The term 'interspace' refers to those parts of the shell between the ribs.

For detailed investigation of the structure of individual layers, specimens have to be used in which the original aragonite is unaltered. Such preservation in British Dactylioceratidae is only found in a restricted area of the Upper Liassic Bifrons Zone clays of western Northamptonshire. Specimens were prepared for examination under a scanning electron microscope (Stereoscan), and all details of the inner shell were revealed. In addition some remarkable dorsal shell layers were discovered, deposited on the venter of the preceding whorl only just in front of the last septum at the rear of the body chamber. These structures partly fill in the spaces between the ribs on the venter of the previous whorl, in a similar fashion to the inner shell which fills in the insides of the same ribs.

II. MATERIAL USED AND PREPARATION

The best material with the original aragonite shell preserved comes from two former brickpits in the *Leda ovum* Beds at Eydon, west Northamptonshire (grid references : SP 535512 and SP 540511). Exposures in the soft clays have long since disappeared, but in the nineteenth century many beautifully preserved specimens of *Peronoceras fibulatum* (J. de C. Sowerby) and *Zugodactylites braunianus* (d'Orbigny) were obtained from the Lower and Middle *Leda ovum* Beds of Fibulatum Subzone, Bifrons Zone age. Most of the specimens consist of fragments of body chambers only, the phragmocone having disappeared, but the final septum and the venter of the previous whorl are preserved in some cases. Two such specimens of *Peronoceras fibulatum* (BM C.67532 and C.77749) provided 23 of the preparations on which this account is based ; both specimens are parts of adult body chambers of about 40–60 mm whorl diameter. Twelve further preparations showing earlier growth stages in septate whorls and immature body chambers of up to 25–30 mm diameter were made from a nodule containing about 50 small specimens (BM C.78546–49 and C.78592–78603) of the same species from the same locality, in which all the whorls are preserved back to the protoconch. Similar aragonite preservation of the same two species occurs in specimens obtained from a former brickpit in the clays of the *Leda ovum* Beds near Badby, Northamptonshire (SP 555586), 8 kilometres (5 miles) NNE of Eydon. An immature example (C.78545) of *Zugodactylites braunianus* from this locality was used to make two preparations of the septate end of the body chamber at about 30 mm diameter.

All the specimens were glued to standard aluminium stubs, then coated with gold prior to examination in the Stereoscan. Pieces of shell taken from various parts of the whorl and mechanically broken to show a clean cross-section were mounted and used without further preparation. Most specimens, however, consist of small portions of shell attached to matrix, cut or broken from the whorls, or whole immature ammonites, which are ground with fine grade silicon carbide, after attachment to the aluminium stub, in order to attain a flat surface or to reach the exact position required in the shell structure. After washing in water, the grinding marks on the surface were removed by etching in dilute hydrochloric acid. In almost all cases application of a 2 per cent solution of HCl for 10–25 seconds was found to be sufficient to remove all traces of grinding from the aragonite part of the surface. Care had to be taken not to dissolve the aragonite shell to a significantly lower plane than the much harder enclosing matrix or secondary calcite, because this resulted in an uneven aragonite surface and difficulties in gold coating and examination in the Stereoscan. Acetate peels were also made from various parts of some Yorkshire Dactylioceratidae that had been cut in half in the plane of coiling. These were used to check the extent of the main and inner shells and the dorsal shell layers. About 800 Stereoscan photographs were taken altogether, and the small proportion reproduced here are those that illustrate the structures to best advantage.

For reasons that are discussed later (p. 63) the nomenclature used in this paper is as follows :

1.	Outer Prismatic Layer	Main shell
2.	Nacreous Layer	
3.	Inner Prismatic Layer	
4.	Outer Prismatic Layer	Inner shell
5.	Inner Nacreous Layer	
6.	Septal Prismatic Layer	

Drawings of the complete shell structure of the near-adult ammonite and of the development of the inner shell during ontogeny are given as Text-figs 1 and 2, in order to facilitate the understanding of the complicated structure.

III. THE MAIN SHELL

The main shell in Dactylioceratidae is the same as in all other ammonites : it consists of a thin Outer Prismatic Layer, a thick Nacreous Layer and a thin Inner Prismatic Layer. On the adult body chambers of the specimens examined the thickness of the main shell is about 0·3 mm at the crests of the ribs and about 0·18 mm at the bottom of the interspaces between ribs, at a whorl diameter of about 50 mm. The bulk of this thickness consists of the Nacreous Layer : the thin tablets of aragonite (Pl. 1, fig. 7) are arranged in vertical columns giving the typical appearance at low magnifications of columnar nacre (Pl. 1, figs 1, 5). The Outer Prismatic Layer is usually not well preserved on the exposed parts of the whorls that were surrounded by the enclosing matrix. It is best seen on the venter of the penultimate whorl, where it is revealed as a very thin layer of vertical prisms of aragonite only about 0·0025 mm thick (Pl. 1, fig. 7). The Inner Prismatic Layer (like all other structures on the inside of the shell) is better preserved, for it was not liable to be removed with the matrix. It is generally much thicker than the Outer Prismatic Layer, being 0·01–0·02 mm thick, and the prisms are noticeably longer (Pl. 1, fig. 6). The adoral edge of the Inner Prismatic Layer was not found in any specimen, but it must be close behind the aperture, because its inner surface is covered by the inner shell which is formed $\frac{1}{8}$ to $\frac{1}{4}$ whorl behind the aperture.

The adult aperture of most species of Dactylioceratidae is constricted by a marked thickening on the inside of the shell. The outer surface of the shell is unaffected, but the Nacreous Layer thickens below the last six to eight ribs until it is three or four times the normal thickness under the penultimate rib. A section through

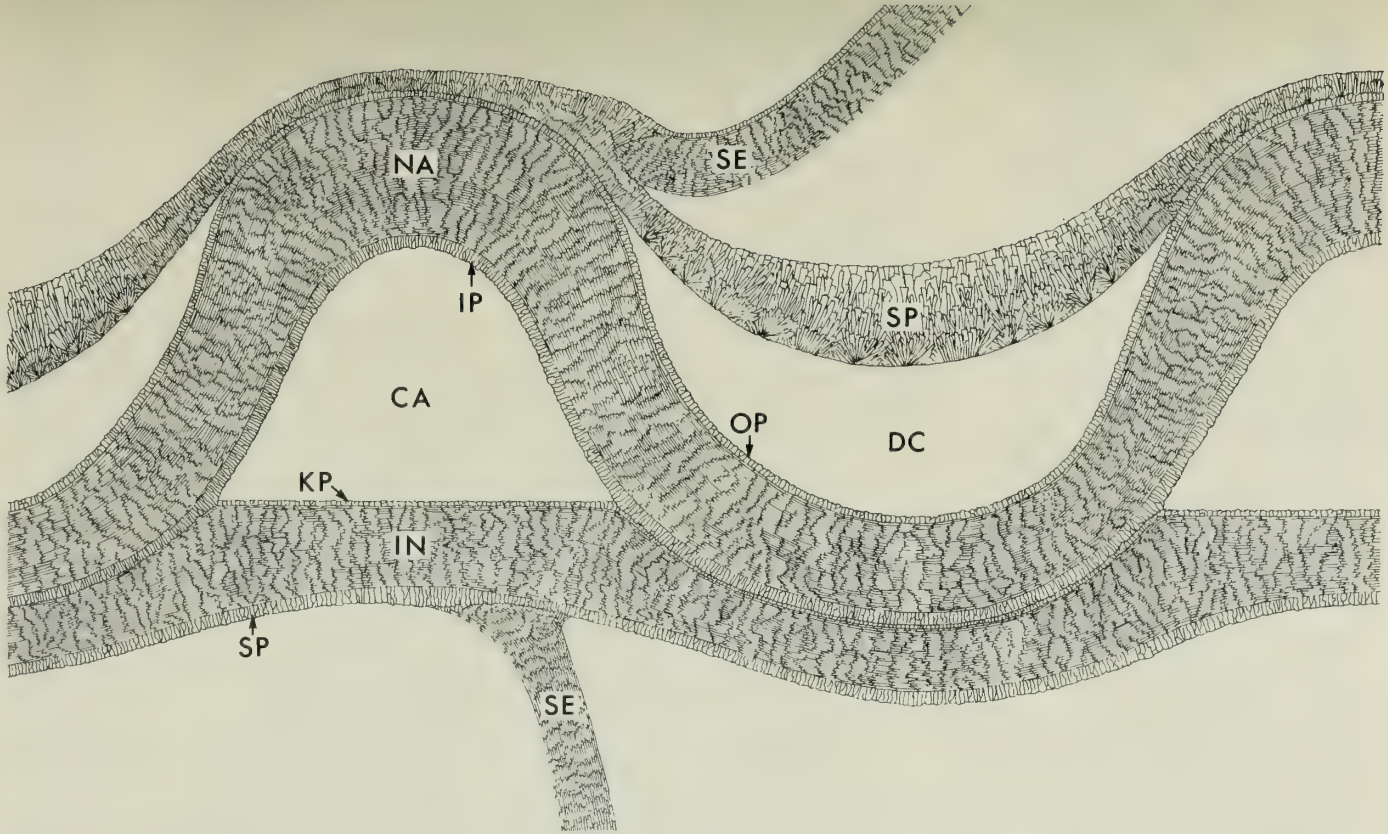


Fig. 1. The full shell structure at the point where the final adult body chamber septum is attached to the middle of the venter of the previous whorl. Shell diameter at final septum c 45 mm; diameter of previous whorl shown here c 28 mm. For abbreviations see p. 67. Drawing based on Pl. 3, fig. 2. The thicknesses of all layers are correct, except for the Inner Prismatic and both Outer Prismatic Layers which are exaggerated for clarity. Note that the Outer Prismatic Layer (KP) of the inner shell is continuous below the middle, but absent below the left-hand, interspace, reflecting the differences observed in specimens. Approx. ×125.

such a constricted aperture was obtained by grinding a Yorkshire coast *Dactylioceras tenuicostatum* (Young & Bird) inside a nodule until the desired position was obtained (Pl. 1, fig. 4). The adoral end of the Inner Prismatic Layer cannot be seen in this fully-grown adult owing to recrystallization. Many specimens show that the constriction affects the whole of the ventral and lateral parts of the aperture. In a few specimens dorsal deposits on top of the venter of the previous whorl can be seen, which correspond in extent with the thickening of the aperture. They sometimes take the form of partitions bridging the spaces between the ribs, as was found in a Yorkshire coast specimen of *Dactylioceras semicelatum* (Simpson) figured in an earlier paper (Howarth 1973 : 251, fig. 4B, partitions P). In this example the dorsal partitions occur only over a short length of the venter of the previous whorl at the adult aperture, and there are none on the dorsum of the rest of the body chamber until the different dorsal deposits of the Septal Prismatic Layer are reached just in front of the final septum.

IV. THE INNER SHELL

The Inner Shell in Dactylioceratidae consists of two layers : a thin Outer Prismatic Layer and a thick Inner Nacreous Layer. The general thickness and development of the layers are similar to those of the main shell, except that the Outer Prismatic Layer has a less well-developed prismatic structure and is not always continuous between the ribs. One of the specimens from Eydon (C.67532) was cut along the middle of the side of the whorl about $\frac{3}{8}$ whorl before the adult aperture, and the precise point of growth of the inner shell was revealed. The front edge of the Outer Prismatic Layer has reached two-thirds of the way across the inside of a rib (Pl. 1, fig. 1) so that the flat floor to this rib cavity is incomplete. This must be the front edge of the inner shell, because the next rib in front has no rib cavity, while the next rib behind has an empty rib cavity floored by a complete partition of the Outer Prismatic Layer of the inner shell (Pl. 1, fig. 5). At higher magnifications this Outer Prismatic Layer is seen to consist of an aragonite sheet with a poorly developed prismatic structure, about 0·0025 mm thick (Pl. 1, fig. 3). The growth of the front edge of the inner shell is not complete on the side of the whorl in this ammonite, so the gradual formation of the Inner Nacreous Layer is seen. The Outer Prismatic Layer occurs alone from its front edge (Pl. 1, figs 1, 3) to just behind the next adapical rib, where the beginning of the Inner Nacreous Layer is seen (Pl. 2, fig. 6) as small plates of aragonite adhering to the inner surface of the Outer Prismatic Layer. Below the next rib adapically the Inner Nacreous Layer has thickened (Pl. 2, fig. 1), and the aragonite plates now being added are as large as those of the Nacreous Layer of the main shell. The layer thickens further and quickly becomes similar in thickness to the Nacreous Layer of the main shell at the same point (Pl. 1, fig. 2).

The junction between the main and inner shells in an interspace on the side of the whorl of C.67532 is illustrated in Pl. 2, fig. 3 ; the obvious parting is between the inner surface of the Inner Prismatic Layer of the main shell and the outer surface of the Outer Prismatic Layer of the inner shell, and the Inner Nacreous Layer is very thin and only partially developed at this point. The Outer Prismatic Layer of the inner shell is not always continuous, however, for on the venter of C.67532, where the inner shell is much more fully grown, the Outer Prismatic Layer only occurs as flat floors to the rib cavities, and is absent between the ribs. In the corners of the rib cavities in this specimen and in C.77749 (Pl. 2, fig. 5) the end of the Outer Prismatic Layer forming the flat floor abuts against the inner surface of the Inner Prismatic Layer of the main shell, and the Inner Nacreous Layer curves round and comes into contact with the same surface. The Outer Prismatic Layer of the inner shell can always be seen forming the floors to the rib cavities, though, especially when a cavity is empty, there is almost always a layer of secondary calcite crystals on top of the floor (Pl. 2, fig. 2).

V. THE DORSAL SHELL

The dorsal shell, which is the overlap of the main shell on to the venter of the previous whorl, is poorly developed in Dactylioceratidae. It is not clear to what extent the Outer Prismatic Layer of the main shell extends on to the venter of the previous whorl, which would have been covered by the thin chitinous periostracum (black layer of *Nautilus*). In some places there is an apparent remnant of the layer or more often merely a parting, but in other places it seems that the Nacreous Layer of the main shell was laid down directly on the venter of the previous whorl. This part of the Nacreous Layer is thin and wedges out within a quarter of the way across the venter, so that the middle half of the venter of the previous whorl is not covered by dorsal shell. In three specimens examined, the Inner Prismatic Layer of the main shell was found not to be a component of the dorsal shell because in each case it wedged out at the umbilical seam contact. The inner shell also wedges out exactly at the umbilical seam contact, and therefore it does not occur at all in the dorsal shell. Pl. 2, fig. 4 shows the dorsal shell above the venter of the previous whorl and the end of the inner shell above the umbilical seam, and Pl. 2, fig. 7 shows the detail of the contact between dorsal shell and venter of the previous whorl. The absence of the Inner Prismatic Layer is apparent in the latter figure and also in Pl. 3, fig. 1. The dorsal shell is fully in contact with the previous whorl at the umbilical seam contact, but further in it bridges across the tops of the ribs of the previous whorl as soon as they have attained any significant relief, then it quickly wedges out. The dorsal shell is formed at the same time as the rest of the main shell, i.e. near the mouth border, and is probably complete before deposition of the inner shell $\frac{1}{8}$ to $\frac{1}{4}$ whorl behind the aperture. A completely different deposit that covers the whole of the dorsum including the dorsal shell is the Septal Prismatic Layer, formed at the rear of the body chamber.

VI. THE SEPTAL PRISMATIC LAYER

A prismatic layer that is closely connected with the formation of the septa is developed in all whorls after the onset of strong ribs, and also occurs on the dorsum of earlier whorls. In the adult it has been investigated in detail in two of the

Northamptonshire specimens : C.77749 was sectioned longitudinally (in the plane of coiling) through the final septum and the adjacent part of the body chamber ; C.78545 was sectioned in the plane of the final septum, then successively further forwards, and finally in a longitudinal plane to reveal the oral end of the layer. The Septal Prismatic Layer is a thick layer of large prismatic crystals which lines the whole of the body chamber. Its point of formation is not more than $\frac{1}{8}$ whorl in front of the final septum, this being a distance roughly equal to the diameter of that septum. On the lateral and ventral parts of the whorl it is attached directly to the inside of the inner Nacreous Layer of the inner shell, with which it maintains intimate contact over the whole surface because of the greatly reduced rib relief of that surface. In septate whorls (Pl. 4, fig. 1) it is a fairly thin layer of parallel prismatic crystals attaining about 0·01 mm in thickness. In adult body chambers the layer is much thicker, attaining 0·05–0·07 mm just in front of the final septum, and thus it may be as thick as the Inner Nacreous Layer to which it is attached. Thus Pl. 4, fig. 2 shows the very thick prismatic layer immediately adjacent to the final septum ; the layer steadily diminishes adorally (Pl. 4, fig. 3 ; Pl. 3, fig. 3) and disappears at its adoral growing edge which is only 12 mm in front of the final septum.

On the dorsum of the whorl the Septal Prismatic Layer takes on a considerably different aspect. It is laid down over the outside of the venter of the previous inner whorl, where the ribs are in full relief, and dorsal shell is absent in the middle of the venter. The layer maintains contact only with the crests of the ribs, and bridges across the spaces between ribs as thick crescent-shaped layers leaving cavities (Text-fig. 1 ; Pl. 3, fig. 4). The cavities themselves are crescent-shaped, unlike the cavities left inside the ribs by the inner shell which always have flat floors. By bridging across in this way the relief of the ribs on the venter of the previous whorl is reduced to approximately half. The second respect in which the dorsal part of the Septal Prismatic Layer differs from the ventral and lateral parts is that even over the crests of the ribs the prismatic crystals do not grow directly on the outside of the Outer Prismatic Layer of the previous whorl, presumably because of the presence of the chitinous periostracum, which is not now preserved, but is represented by a parting or secondary material. So the prisms of the Septal Prismatic Layer grow from a few centres of crystallization as radiating bunches of small prisms, becoming larger and sub-parallel when adjacent bunches touch and intermingle (Pl. 3, fig. 6). The crescent-shaped parts of the layer between the ribs are much thicker and the radiating bunches giving rise to large prismatic crystals are more marked (Pl. 3, fig. 5). At the edge of the dorsum there is a transition zone between the mid-dorsum part and the side of the whorl part of the Septal Prismatic Layer : here the main shell Nacreous Layer forms the dorsal shell, and the Septal Prismatic Layer is attached directly to its inside surface (Pl. 3, fig. 1).

The septa are a direct development of the Septal Prismatic Layer. At the point of attachment of a septum anywhere around its edge the large prismatic crystals of the Septal Prismatic Layer change almost instantaneously into the nacreous crystals of the septum (Pl. 4, figs 4–6). The septum is not usually added to the inside of the Septal Prismatic Layer ; rather, it is a continuation of the growth of that layer, which is thickened immediately adoral to the septum by approximately the thickness of the septum. This added thickness diminishes gradually until the point of attachment of the next septum is reached. On the dorsum, however, there is sometimes evidence of discontinuities within the Septal Prismatic Layer, perhaps indicating that it started growth somewhat before the lateral and ventral parts of the layer, and the septum may be added on to the inside. Thus Pl. 4, fig. 6 shows a septum attached to a mid-dorsal part of the Septal Prismatic Layer which is divided by partings into two layers at one side of the confluence and three layers at the other side ; further to the left of the confluence the two layers become equal in thickness. The mid-dorsum in another specimen has a normal single Septal Prismatic Layer, thin over the rib crests (Pl. 5, fig. 1) and much thicker between the ribs (Pl. 5, fig. 4), which is succeeded by a thin smooth layer with a marked 'building-block' structure in some places, and the septum is attached to the inside of the building-block layer (Pl. 5, fig. 1). At the point of attachment the nacre of the septum changes rapidly into a thick mass of prismatic crystals (Pl. 5, fig. 1) which diminishes in thickness adorally (Pl. 5, fig. 4) and disappears before the crest of the next rib (Pl. 5, fig. 5), where the building-block layer alone is attached to the inside of the Septal Prismatic Layer.

Formation of the Septal Prismatic Layer was found to be more irregular on the dorsum of one specimen. In some places the crescent-shaped layers between the ribs are thicker than usual, and they are formed by growth of radiating masses of prisms in the upper half of the layer, as well as the usual growth of prisms from the base (Pl. 6, fig. 1). In almost all cases this leaves cavities, which are sometimes very large, in the middle of the Septal Prismatic Layer (Pl. 5, fig. 2). In another part of the same specimen two Septal Prismatic Layers are formed between the ribs (Pl. 6, fig. 2) : the first layer is almost in contact with the outer surface of the shell, but it is truncated before reaching the tops of the ribs by a second layer which passes over the ribs, and passes from crest to crest of the ribs leaving cavities below like the normal development of the Septal Prismatic Layer. This type of double layer can be explained by a movement of the mantle surface to a higher position between the ribs after it had initiated secretion of the first layer lower down. Occasionally radiating masses of prismatic crystals are formed in the cavity below a Septal Prismatic Layer that is otherwise normally developed (Pl. 6, fig. 3).

Most of the septa that have been examined in these adult or near-adult specimens consist of a single layer of nacreous crystals, but the final adult body chamber septum in C.77749 (Pl. 3, fig. 2) also has a thin adoral layer of prismatic crystals (Pl. 5, fig. 3).

VII. ONTOGENETIC DEVELOPMENT

The above descriptions of main shell, inner shell, Septal Prismatic Layer and septa were taken from adult or near-adult body chambers of two specimens of *Peronoceras fibulatum* and one of *Zugodactylites braunianus*. Light microscope examination of the shell surface and sectioned specimens of many other species of Dactylioceratidae suggests that these are constant features that apply to all whorls after the onset of strong ribs. In many Dactylioceratidae that have approximately seven whorls up to the adult mouth border, this refers to the outer 3–3½ whorls from a diameter of approximately 10 mm upwards. Earlier growth stages, from the mouth of the protoconch through the smooth early whorls and up to the formation of the ribs, have a simpler structure, which was investigated with a view to tracing the development of the inner shell. For this purpose twelve immature specimens of *P. fibulatum* were sectioned to reveal the inner whorls, some having body chambers at less than 6 mm maximum whorl diameter. The larger whorls on six of them confirmed that the shell structure after strong ribs are fully developed is the same as in the adult. The description that follows is based on six specimens that were sectioned in the plane of coiling through the centre of the protoconch, and two that were sectioned to expose a spiral surface passing through the middle of the side of the whorl, to show the commencement of ribs on the whorl side.

(a) *Protoconch, first whorl and nepionic constriction*

The shell structure of early growth stages has been described for several different ammonites by Birkelund (1967), Birkelund & Hansen (1968), Erben, Flajs & Siehl (1969) and Drushits & Khiami (1970). All the Dactylioceratidae that have been investigated are similar. The protoconch wall consists of a single layer of sub-prismatic crystals (Pl. 6, fig. 4). Just before the mouth of the protoconch a second similar layer appears on the inside (Pl. 5, fig. 6), and the first layer wedges out close to the protoconch mouth (Pl. 7, figs 2, 3). The second prismatic layer then thickens and forms the wall of the first whorl up to about $\frac{1}{16}$ whorl before the nepionic constriction (Pl. 6, fig. 6). In five different specimens the nepionic constriction occurs $\frac{13}{16}$ whorl after the mouth of the protoconch. About $\frac{1}{16}$ of a whorl earlier a nacreous layer is added to the inside of the prismatic layer, which itself diminishes considerably in thickness (Pl. 6, fig. 5). At the nepionic constriction the prismatic layer is folded back on itself through 180 degrees, a new prismatic layer starts on the inside of the nacreous layer and cuts obliquely across touching the inside of the folded-back part of the old prismatic layer, then reaches the outside of the shell and continues forwards as the Outer Prismatic Layer of the main shell (Pl. 7, fig. 1). The Nacreous Layer of the main shell is added on the inside starting near the commencement of the Outer Prismatic Layer.

(b) *Smooth whorls after the nepionic constriction*

Between the nepionic constriction, $\frac{13}{16}$ whorl after the mouth of the protoconch, and the start of the ribs at 2¼–2½ whorls on the side of the whorl and 3–3¼ whorls on the venter, there are 1½–2 whorls without ornament. At first the Outer Prismatic and the Nacreous Layers are of approximately equal and steadily increasing thickness (Pl. 7, fig. 7). The start of the Inner Prismatic Layer occurs at 1¼–1¾ whorls, where the shell has reached a total thickness of about 0·02 mm (Pl. 7, fig. 8). The Inner Prismatic Layer has noticeably smaller prisms at first than the Outer Prismatic Layer ; it increases rapidly in thickness, partly at the expense of the Nacreous

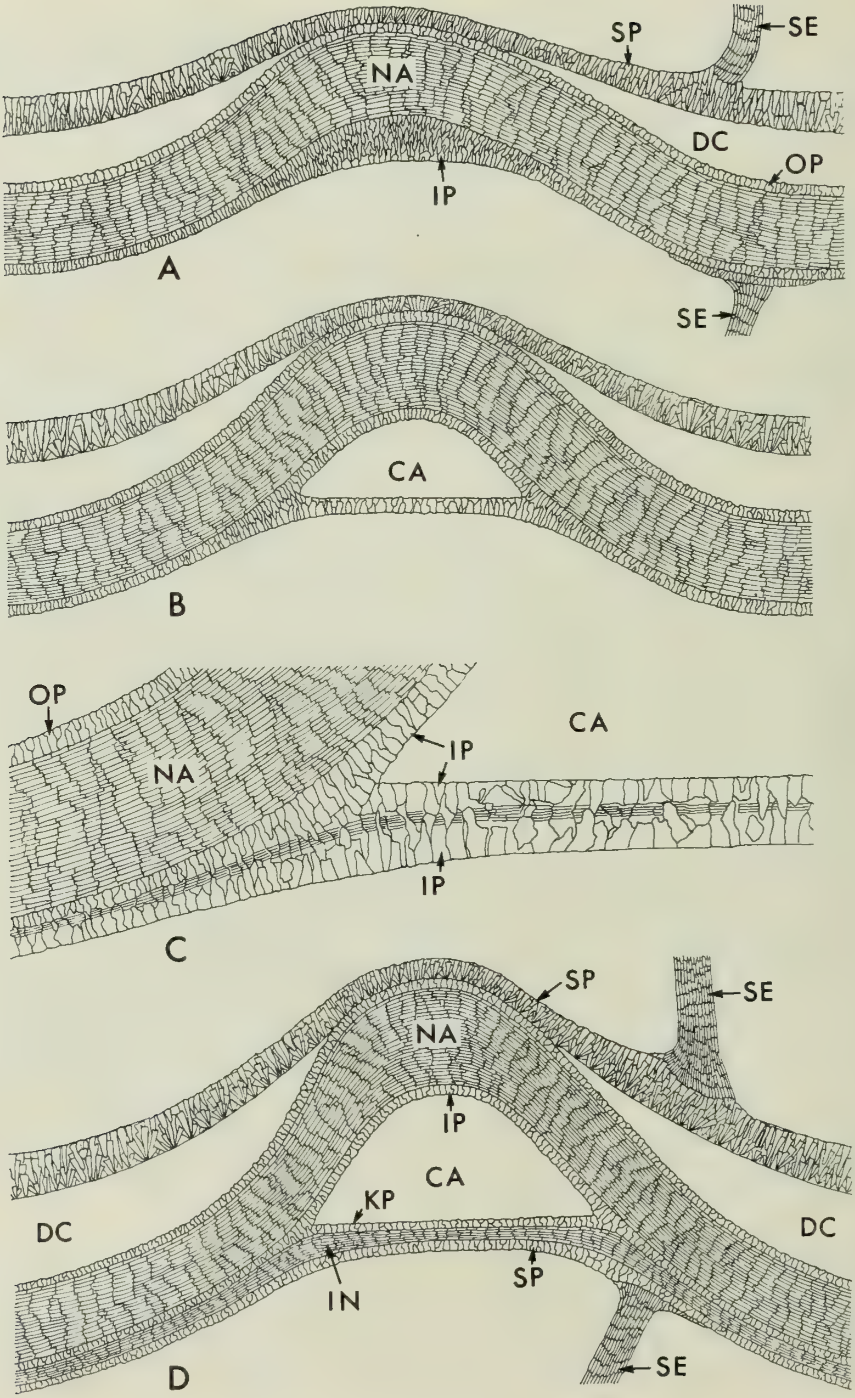
Layer (Pl. 7, fig. 5), and at about 2 whorls it is much thicker than the Outer Prismatic Layer (Pl. 7, fig. 9). The Nacreous Layer then thickens again, so that by the time the ribs commence at $2\frac{1}{4}$–$3\frac{1}{4}$ whorls it is the thickest of the three layers, and the total shell thickness is about 0·06 mm (Pl. 7, fig. 6).

(c) *Development of the ribs and the inner shell*

Ribs commence on the side of the whorl at $2\frac{1}{4}$–$2\frac{1}{2}$ whorls and about 3 mm shell diameter. The venter remains smooth for a further $\frac{3}{4}$ whorl, then ventral ribs begin at 3–$3\frac{1}{4}$ whorls and 5–6 mm shell diameter. The ribs start as low undulations and increase slowly in strength, and a rough assessment is that the ribs on the side of the whorl take 1–$1\frac{1}{4}$ whorls until the amplitude equals half the crest to mid-trough distance (half the wavelength), while the ribs on the venter attain the same amplitude after about $\frac{3}{4}$ whorl. The shell structure of the previous smooth whorls remains unaltered during most of the development of the ribs on the side of the whorl (Pl. 8, fig. 4). Changes in the structure commence when the ventral ribs begin to develop at about $3\frac{3}{8}$ whorls and 7 mm diameter, and they affect the ribs on both the venter and the side of the whorl equally. First the Inner Prismatic Layer becomes thicker underneath the rib (Pl. 8, fig. 1). After only one to three further ribs the Inner Prismatic Layer splits in the middle (Pl. 8, figs 2, 3) ; the outer part remains in contact with the Nacreous Layer below the crest of the rib, while the inner part forms a flat floor across the inside of the rib leaving a cavity above. This is the first appearance of cavities inside the ribs, and at this stage the cavities are, in fact, inside the Inner Prismatic Layer. After a further period of growth and increase in size of the ribs, which varies between a few ribs and about $\frac{1}{4}$ whorl, the first signs of a nacreous layer begin to appear in the middle of the Inner Prismatic Layer. This is the start of the Inner Nacreous Layer of the inner shell. In those parts of the shell between the ribs, small flat plates of nacre develop in the middle of the Inner Prismatic Layer (Pl. 8, fig. 5). Similar plates of nacre develop in the middle of the prismatic layer that forms the floor to each rib cavity (Pl. 8, fig. 6). The rib cavity floors are now divided into three parts : the prismatic layer that forms the floor itself and henceforth is called the Outer Prismatic Layer of the inner shell ; at these early growth stages it occurs only below rib cavities, but later it occurs between the ribs as well, and is clearly added to the inside of a fully grown Inner Prismatic Layer (Pl. 2, fig. 3). The middle layer is the Inner Nacreous Layer which thickens steadily during further ontogenetic development (Pl. 9, figs 1, 2) until it attains a thickness comparable with its development in the adult (Pl. 9, fig. 4). The third layer is the innermost prismatic layer, which soon becomes closely connected with the attachment of the septa (Pl. 9, fig. 3) and merges with the Septal Prismatic Layer that is already present on the dorsum.

(d) *Insertion of septa and development of the Septal Prismatic Layer*

The proseptum and primary septum are at the mouth of the protoconch and consist of prismatic crystals. The next septum (Pl. 7, fig. 2) and all succeeding septa consist of nacreous crystals. At the point of attachment to the shell wall the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structure of each septum changes rapidly to prismatic crystals. At the dorsal part of the septal attachment (i.e. the attachment to the outside of the venter of the previous whorl) the prismatic crystals form a continuous layer which extends from septum to septum and is called the Septal Prismatic Layer. The lateral and ventral parts of the septal attachment consist of a small 'foot' of prismatic crystals which does not extend far along the inside of the shell wall. However, after the onset of ribs and the formation of the Inner Nacreous Layer, the Septal Prismatic Layer spreads from its original dorsal position to line the whole of the lateral and ventral parts of the inside of the shell, and each septum is now a direct development of that layer all around its periphery (Pl. 4, figs 4–6). Illustrations of the ventral part of the septal attachment are as follows : immediately after the mouth of the protoconch, Pl. 7, fig. 3 (this is the first septum) ; attachment to the inside of the nacreous layer immediately before the nepionic constriction, Pl. 6, fig. 5 ; to the inside of the Nacreous Layer after the nepionic constriction but before the Inner Prismatic Layer develops, Pl. 7, fig. 4 ; to the inside of the Inner Prismatic Layer, Pl. 10, fig. 4 ; to the inside of the Inner Prismatic Layer during the early stages of rib formation, Pl. 9, fig. 5 ; and finally, after development of the Inner Nacreous Layer, the septa are in continuity with much of the thickness of the Septal Prismatic Layer, which now lines the inside of the venter (Pl. 8, fig. 7) as well as the lateral and dorsal parts of the whorl. At larger sizes ventral septal attachment has already been shown in Pl. 4, fig. 5.

The Septal Prismatic Layer first appears on the dorsum in the first whorl after the protoconch. It probably occurs continuously from the mouth of the protoconch, but in the material available it is first seen just over one whorl after the protoconch as a continuous thin layer added on top of the previous whorl (Pl. 7, fig. 3). The continuity of the Septal Prismatic Layer is more apparent about a $\frac{1}{2}$ whorl later where another septum is attached (Pl. 6, fig. 6), and it is quite clear at the nepionic constriction (Pl. 7, fig. 1), where it is seen to extend between two septa attached to the outside of the shell and consists of small prismatic crystals. It occurs in this form as a continuous dorsal layer throughout the next few whorls, though it is sometimes missing or detached from the outside of the venter of the previous whorl owing to faulty preservation, such as in Pl. 7, fig. 5. A dorsal septal attachment

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FIG. 2. Series illustrating the development of the inner shell, based on C.78594 and C.78598, at shell diameter of c 6·5 mm ; for abbreviations see p. 67.

A – Inner Prismatic Layer considerably thickened below rib ; septum on inside has foot of prismatic crystals attached to fully formed Inner Prismatic Layer ; dorsal Septal Prismatic Layer and a septum in the next outer whorl above the rib. × 275.

B – Two ribs adoral to A ; Inner Prismatic Layer now divided and part of it forms the floor below the hollow rib. × 275.

C – Eight ribs adoral to A ; first appearance of the nacreous crystals of the Inner Nacreous Layer in the middle of the Inner Prismatic Layer. × 750.

D – About 15 ribs adoral to A ; Inner Nacreous Layer now well formed, and ventral part of the Septal Prismatic Layer on the inside shows some continuity with the septum ; dorsal Septal Prismatic Layer of the next outer whorl on the outside shows considerable continuity with the septum. × 275.

two whorls after the protoconch is shown in Pl. 10, fig. 5, and another to the shell at the point where ribs first commence is seen in Pl. 9, fig. 5. As soon as the Septal Prismatic Layer is laid down on top of ribs that have attained significant relief, it no longer maintains contact with the outside surface of the shell between the ribs, but bridges across the tops of the ribs leaving slender cavities below (Pl. 10, fig. 1). At this stage the Septal Prismatic Layer consists of longer prisms radiating in bunches from the bottom surface of the layer (Pl. 10, fig. 3), and septa are continuous with the outer part of the layer (Pl. 10, fig. 2). Further development consists of thickening of the Septal Prismatic Layer until it attains the appearance in the adult as already described.

(e) *Position of secretion of individual layers*

The Outer Prismatic Layer and the Nacreous Layer of the main shell are secreted at the mouth border by the front edge of the mantle. In order to maintain strength and rigidity, formation of the Nacreous Layer must proceed very quickly behind the Outer Prismatic Layer ; in fact it seems probable that the necessary strength and immunity from injury could only be attained by growth to full thickness in the space of one or two ribs behind the mouth border. The position of formation of the Inner Prismatic Layer changes during ontogeny. In an immature specimen which had a body chamber at a stage before the development of ventral ribs, the Inner Prismatic Layer was formed in the apical half of the body chamber, but sufficiently so far forwards that when the septa were inserted they were added to the inside of a fully formed Inner Prismatic Layer. During development of the ribs and the inner shell, the point of formation of the Inner Prismatic Layer moves further forwards in the body chamber, because it is always in front of the growing edge of the inner shell. During early stages of rib formation the layer is secreted at about the middle of the body chamber, but by the time the adult is reached secretion occurs only $\frac{1}{8}$ whorl behind the mouth border.

When the inner shell was first formed the two constitutent layers (the Outer Prismatic Layer and the Inner Nacreous Layer) were secreted $\frac{1}{4}$–$\frac{3}{8}$ whorl in front of the last septum. As growth proceeded, the position of secretion moved steadily forwards in the body chamber, until it was formed $\frac{1}{8}$–$\frac{1}{4}$ whorl behind the mouth border in the adult. The formation of the inner shell by division of the original Inner Prismatic Layer left the inner half of that layer on the inside of the body chamber. Observations on three immature specimens suggest that as soon as the Inner Nacreous Layer had grown to a significant thickness (i.e. equal to that of the original Inner Prismatic Layer), then secretion of the prismatic layer on the inside moved quickly back to a position just in front of the final septum, where it merged with the Septal Prismatic Layer which was already present on the dorsum. The Septal Prismatic Layer now formed a complete lining to the body chamber and was closely connected with the insertion of septa. In small immature ribbed specimens this layer extends only one or two rib widths in front of the last septum, while in larger specimens and in the adult body chamber the front growing edge of the layer is up to $\frac{1}{8}$ whorl in front of the last septum. The position of formation of the Septal Prismatic Layer on the dorsum in small whorls before the development of ribs could not be determined from the material available, but by analogy it was probably formed just in front of the last septum.

VIII. OCCURRENCE OF INNER SHELL

(a) *Dactylioceratidae*

The presence of an inner shell has been observed in all Dactylioceratidae that are sufficiently well preserved to show the shell structure. In the Upper Lias it is present in *Dactylioceras* (*Orthodactylites*) from the Tenuicostatum Zone (Howarth 1973), many different species of *D.* (*Dactylioceras*) from the Exaratum, Falciferum and Commune Subzones, and in the genera *Nodicoeloceras*, *Peronoceras*, *Zugodactylites*, *Porpoceras*, *Catacoeloceras* and *Collina* (Guex 1970). No well-preserved specimens have been seen that do not have an inner shell. In many examples of *Dactylioceras* (*Orthodactylites*) from the Tenuicostatum Zone of the Yorkshire coast, *Dactylioceras commune* (J. Sowerby) from the Yorkshire Commune Subzone and *Peronoceras* and *Zugodactylites* from the Northamptonshire *Leda ovum* Beds, it can be seen that the front edge of the inner shell is between $\frac{1}{8}$ and $\frac{1}{4}$ whorl behind the adult mouth border. No differences between genera and species have been detected in this respect, and in many specimens it can be seen that the front edge of the inner shell is similar in shape to the mouth border, i.e. approximately radial, but there is no rostrum on the venter. An inner shell is also developed in the Lower Liassic genus *Prodactylioceras*, for several well-preserved examples from the Davoei Zone of the Dorset coast, Gloucestershire and Oxfordshire show the hollow ribs of the main shell and the flat-topped ribs of the inner shell very well. In this genus the inner shell does not appear to extend further forwards than $\frac{1}{2}$ whorl behind the mouth border. No Middle Liassic Dactylioceratidae of the genera *Prodactylioceras* and *Reynesoceras* have been seen that are sufficiently well preserved to show the shell structure, and this is the only significant group in which the presence of an inner shell has yet to be proved.

(b) *Other ammonites*

Many other well-preserved Jurassic and Cretaceous ammonites have been examined, but an inner shell like that in the Dactylioceratidae has not yet been found in any other group. Middle and Upper Jurassic Perisphinctidae are the most likely group to have an inner shell, for some of them are homeomorphs of Dactylioceratidae, but in a number of very well-preserved examples from different horizons it can be shown that only a main shell is present. This is based on optical microscope examination, where it is seen that there are no rib cavities and that the shell is of uniform thickness, but electron microscope confirmation of the absence of an inner shell has not been made. There are, however, structures in some members of the Middle and Upper Triassic family Trachyceratidae that can only be due to the development of an inner shell like that in Dactylioceratidae. They are shown by *Maclearnoceras enode* Tozer and *Frankites sutherlandi* (McLearn), both from the Upper Ladinian of British Columbia (Tozer 1967 : 29–30, pl. 8, figs 8–12 ; 1972 : 640–641, fig. 2, pl. 128, figs 3–9). The inner shell lines the body chamber, and ends only a short distance behind the aperture, where an abrupt transition is seen on the internal mould between the strong ornament on the inside of the main shell and the much weaker ornament on the inside of the inner shell. The inner shell is in contact with the whole of the inside surface of the main shell, so that cavities are not formed inside the ribs. *Maclearnoceras* has strong ribs on the main shell, but the inner surface of the inner shell is completely smooth. In *Frankites* the ribs are less strong and are reduced, but still present, on the inside of the inner shell. It is possible that an inner shell is a feature of many Trachyceratidae, and well-preserved aragonite material would be worthy of electron microscope investigation.

Other structures that are widely developed in Jurassic and Cretaceous ammonites, and which might be comparable with the inner shell or the Septal Prismatic Layer of Dactylioceratidae, are floors below hollow keels and spines, and dorsal shields. Hollow keels and spines cut off by floors have been frequently observed (Hölder 1952). The structure of the floors was first investigated in detail by Erben (1972), who showed that they were part of the Inner Prismatic Layer. The spine floors figured by Erben (1972 : pl. 1, fig. 1 ; pl. 2, fig. 1 ; pl. 3, fig. 1) bear a close resemblance to the rib floors in Dactylioceratidae when they first appear and are formed by splitting of the Inner Prismatic Layer (Pl. 8, fig. 2). They differ, however, in having one or more chitinous membranes within that layer, which divide the prismatic layer that lines the inside of the spine from another layer added on the inside of the spine again and then also forms the flat floor below the spine. The conchiolin membranes indicate time pauses between the separate layers, and it is possible that only the outermost layer is properly called the Inner Prismatic Layer, while the layer forming the floor may be more comparable with the Septal Prismatic Layer, having been formed further back in the body chamber. Keel floors were also figured by Erben (1972 : pl. 3, figs 2, 3 ; pl. 4) and consist of a thick prismatic layer. However, the prismatic structure of the floor is not apparent from Erben's figures, so a preparation of the same material was made and investigated. Pl. 9, fig. 6 shows the hollow keel and floor of *Eleganticeras elegantulum* (Young & Bird) from Glacial Drift, *ex* Upper Lias at Ahrensburg, Germany. It is from the end part of the phragmocone just before the body chamber, at a shell diameter of about 50 mm. The floor consists of a thick prismatic layer which is continuous with the Inner Prismatic Layer that lines the inside of the keel above the cavity. Other preparations confirm that there is no discontinuity in the prisms where the floor meets the lining inside the keel, and they also show that this is the Inner Prismatic Layer that is attached direct to the inside of the Nacreous Layer. There are considerable resemblances with the Septal Prismatic Layer in Dactylioceratidae, and it is clear that whenever features such as keels and spines are to be smoothed out before insertion of the septa, this can be done by further growth of the Inner Prismatic Layer in the rear part of the body chamber.

The term 'dorsal shield' was used by Casey (1962 : 264) for a layer secreted on the dorsum of the body chamber in *Douvilleiceras* to smooth out the very large tubercles of the venter of the preceding whorl. It bears some resemblance to the dorsal development of the Septal Prismatic Layer in Dactylioceratidae, inasmuch as the layer bridges between the crests of the ribs and the tubercles leaving cavities below.

Details of the structure of the layer and its point of formation within the body chamber have yet to be investigated. Somewhat similar are the spirally ornamented dorsal layers of *Amaltheus* (Walliser 1970 : pl. 4, fig. 5) and *Discotropites* (Tozer 1972 : 642). They may be part of the Inner Prismatic Layer or another prismatic layer added later, but details of their structures are not known.

IX. NOMENCLATURE

The nomenclature used in this paper for the individual layers of the Dactylioceratidae shell has been given on p. 50. For the main shell it is in accordance with the general consensus of opinion of most authors who have described shell structure recently, and in particular it has been used by Birkelund & Hansen (1968, 1974), Erben, Flajs & Siehl (1969), Drushits & Khiami (1970) and Erben (1972). This nomenclature has also been used successfully for *Nautilus* and fossil nautiloids (Erben, Flajs & Siehl, 1969 : 6). Terminology used by some other authors involves the adjectives 'porcellaneous' or 'spherulitic' instead of 'prismatic' for the inner and outer layers, and various uses of the terms 'ostracum' and 'hypostracum'. It is hoped that the nomenclature can now be stabilized and that the terms 'Inner Prismatic Layer' and 'Outer Prismatic Layer' will be used. There is little to be gained by use of the terms 'ostracum' or 'hypostracum' as alternatives for different divisions of the main shell, especially as they have been applied in conflicting senses by different authors (Stenzel, 1964 : K77 ; Erben, Flajs & Siehl, 1969 : 6), and their application to fossil cephalopods is not recommended. The term 'periostracum' is to be retained, however, for the organic (conchiolin) layer deposited dorsally just in front of the aperture in *Nautilus*. This is the 'black layer', and was probably present in ammonites. These are the terms that will be used in the projected revision of the Ammonoidea volume of the *Treatise on Invertebrate Paleontology*.

In view of the consistent nomenclature now used by most authors, it is unfortunate that different terms were used recently for Triassic ammonites by Tozer (1972), which will lead to confusion if perpetuated. His 'Outer Test' and 'Inner Test' were derived from Casey's (1961 : 178) 'outer layer of test', proposed originally for the Outer Prismatic Layer and the Nacreous Layer, and his 'inner layer of test', proposed for the Inner Prismatic Layer which alone forms the dorsal wall of the shell in some ammonites. However, Tozer used 'Outer Test' for the Outer Prismatic Layer only, and 'Inner Test' for the Nacreous and Inner Prismatic Layers. They are unnecessary terms, for the shell layers are more exactly described by the terms Outer Prismatic, Nacreous and Inner Prismatic Layers, even when the detailed structure cannot be seen owing to recrystallization, because enough can usually be deduced by comparison to relate the shell to those layers. Tozer also referred to his 'Inner Test' as 'secondary deposits', because it was deposited after the Outer Prismatic Layer. But the Nacreous and Inner Prismatic Layers are not secondary in a diagenetic sense, and the term 'secondary deposits' is better reserved for the secondary deposits of calcite that are frequently formed inside cephalopod septal chambers during the process of fossilization.

The choice of suitable terminology for the extra layers in Dactylioceratidae presents some difficulties. Guex's (1970 : 339) term 'Preseptal Layer', which was adopted by Tozer (1972 : 640), is unfortunate now that electron microscope investigation has revealed that three new layers are added, and it is better to use terms that describe their structural appearance. Outer Prismatic Layer is used for the layer that forms the floors to the rib cavities, and Inner Nacreous Layer for the thick layer formed immediately afterwards ; these two layers form the Inner Shell, a term first used by Howarth (1973 : 250) to describe the inner of the two shells that are so clear in any well-preserved Dactylioceratidae. At a later stage the last shell layer, the Septal Prismatic Layer, is formed at the rear of the body chamber, and is so called because of its continuity with the septa. This terminology results in two Outer Prismatic Layers in the shell of Dactylioceratidae, one in the main shell, the other in the inner shell, but different terminology for the four prismatic layers leads to worse complications, especially when the structure is traced through ontogeny or compared with shells of normal ammonites. It is highly desirable to retain the normal terminology for the main shell, and then all the changes in nomenclature that occur when the Inner Prismatic Layer splits up during ontogeny are confined to those layers added on the inside that are unique to Dactylioceratidae.

X. FUNCTION OF THE INNER SHELL

The function of the inner shell can only be a matter for speculation, and Tozer (1972 : 641) has discussed some of the possibilities. It is probable that its function was similar to that performed by dorsal shields and by the septa which cut off keels and spines in other ammonites. All these structures served to eliminate or reduce the relief of morphological features that might impede movement of the ammonite. In the case of a long spine, once deposition of the main shell was complete, the ammonite would withdraw the mantle from contact with the inside of the spine, probably because a bulge of mantle and soft parts into the spine would interfere with the forward movement prior to the formation of a new septum. Instead, the mantle was stretched across the base of the liquid-filled spine, and this was sufficient to reactivate deposition of shell material at the mantle surface. By cutting off spines and keels in this way the inside of the body chamber was smoothed, so that forward movement during growth was easier and the septa could be attached to a more even surface. The complete inner shell in Dactylioceratidae seems to have been an extension of such extra shell deposition and was probably merely fortuitous to that family.

If smoothing of the inside of the body chamber was the main result of the acquisition of an inner shell, then other effects would be alteration in the strength and weight of the shell and in its attitude during life. The strength of the shell would be increased because of the box effect of the hollow ribs. The weight would also be increased, and must have been compensated for by reducing the amount of liquid in the chambers of the phragmocone. An alternative explanation is that Dactylioceratidae may have had considerably thinner main shells than other ammonites, so that the total weight of the shell was not increased, but there is no comparative data on this point. The attitude of the shell when in buoyant equilibrium in sea-water would have been affected because inner shell is absent in the last $\frac{1}{8}$–$\frac{1}{4}$ whorl before the aperture. This final portion would be relatively lighter than the rest of the shell in which the inner shell is complete, and the equilibrium position would then be with the aperture held higher than in a normal ammonite. This may have been somewhat disadvantageous for Dactylioceratidae if the resulting position was with the aperture pointing nearly vertically upwards.

Acknowledgements. Thanks are due to Mr B. S. Martin and Mr C. G. Ogden and their staff of the Electron Microscope Unit of the British Museum (Natural History) for their training and constant encouragement in the use of the Cambridge Instrument Co's Stereoscan Mk IIA and Stereoscan 600 electron microscopes, without which this investigation would not have been possible.

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PLATES

The following specimens are figured in the plates where they are referred to by their registered numbers :

C.67532. *Peronoceras fibulatum* (J. de C. Sowerby). Upper Lias, Bifrons Zone, Eydon Brickpit, Northamptonshire. Half a whorl of adult body chamber at 45–60 mm whorl diameter, but mouth border and final septum missing.

C.77749. Same as C.67532. Apical half whorl of adult body chamber and final two septa at 40–55 mm whorl diameter.

C.78592–78603. Same as C.67532. From a small nodule containing about 50 immature specimens with body chambers at many different stages of ontogeny.

C.78545. *Zugodactylites braunianus* (d'Orbigny). Upper Lias, Bifrons Zone, Badby, Northamptonshire. Final septum and $\frac{3}{4}$ whorl of body chamber of an immature example at 25–40 mm whorl diameter.

Abbreviations used for the shell layers :

OP	Outer Prismatic Layer	Main shell
NA	Nacreous Layer	
IP	Inner Prismatic Layer	
KP	Outer Prismatic Layer	Inner shell
IN	Inner Nacreous Layer	
SP	Septal Prismatic Layer	
SE	Septum	
CA	Cavity inside a rib cut off by the inner shell	
DC	Cavity between dorsal Septal Prismatic Layer and an interspace on venter of the previous whorl	

All the figures are of mid-ventral sections cut in the plane of coiling, unless otherwise stated. All are scanning electron micrographs, except Pl. 1, fig. 4.

PLATE 1

Peronoceras fibulatum (J. de C. Sowerby)

FIG. 1. Rib with incomplete flat floor formed by the Outer Prismatic Layer of the inner shell in which a gap is left on the adoral (left) side of the rib ; rib cavity above floor filled with matrix. C.67532. × 85 (pp. 50, 52)

FIG. 2. Fully developed inner shell leaving an empty cavity within a rib ; thickness of inner shell below rib equals that of main shell, thickness between ribs about half that of main shell. C.77749. × 47·5. (p. 52)

FIG. 3. Enlargement of middle of rib cavity floor in Fig. 1, showing thin Outer Prismatic Layer of inner shell. C.67532. × 1600. (p. 52)

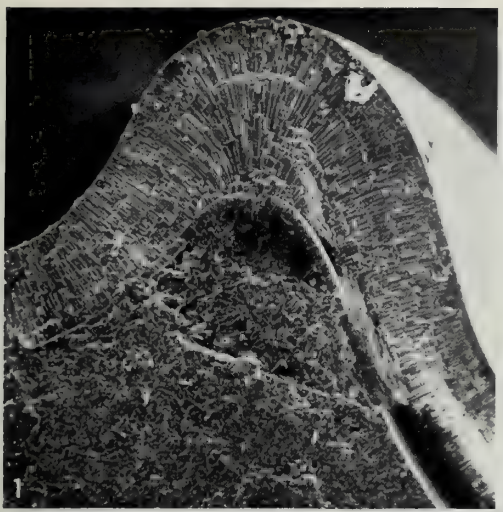
FIG. 5. Next rib adapical to Fig. 1 ; rib floor now complete and cavity empty. × 110. (pp. 50, 52)

FIG. 6. Enlargement of part of Fig. 5, showing Inner Prismatic Layer below Nacreous Layer on inside of rib, and rib cavity at lower left. × 800. (p. 50)

FIG. 7. Outside surface of main shell ; thin Outer Prismatic Layer and part of Nacreous Layer below. C.67532. × 1600. (p. 50)

Dactylioceras (Orthodactylites) tenuicostatum (Young & Bird)

FIG. 4. Upper Lias, Whitby, Yorkshire. Section through mid-venter of adult mouth border, showing thickening of inside of main shell below the last eight ribs, which forms the constriction at the mouth border seen only on the internal mould ; thickening consists of additional material of the Nacreous Layer. C.3041. Optical photograph, × 5·5. (p. 52)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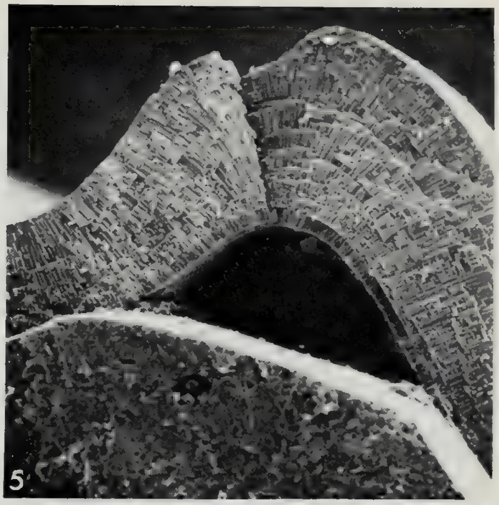
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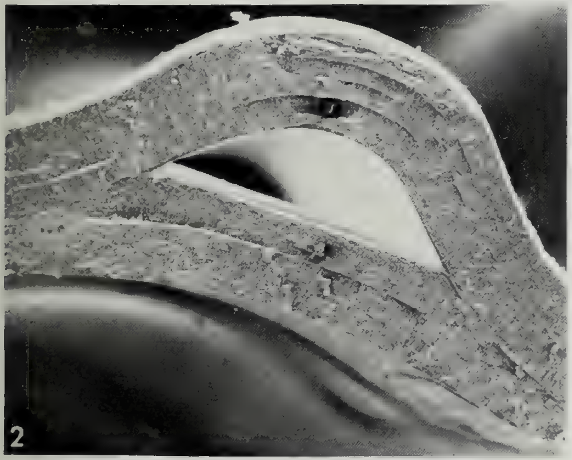
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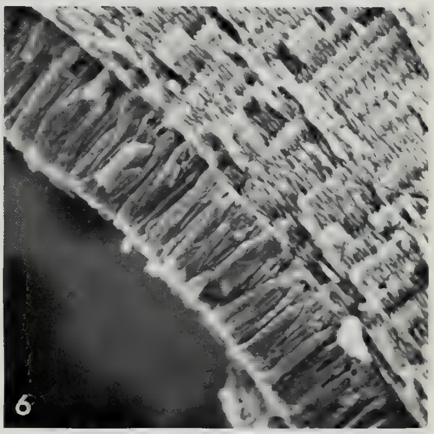
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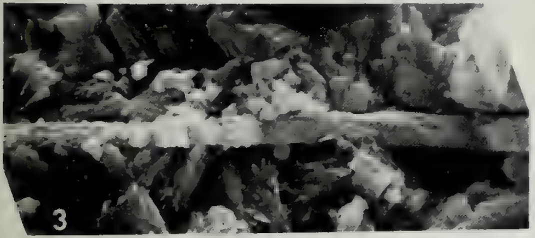
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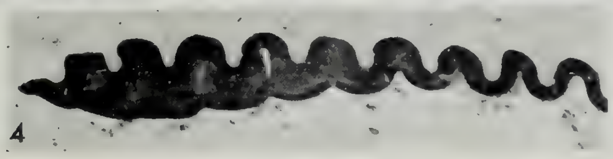
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PLATE 2

Peronoceras fibulatum (J. de C. Sowerby)

FIG. 1. Floor below rib cavity ; thin Outer Prismatic Layer of inner shell, and Inner Nacreous Layer below. C.67532. × 3250. (p. 52)

FIG. 2. Floor of rib cavity as in Fig. 1 ; thin Outer Prismatic Layer of inner shell overlain by large crystals of secondary calcite. C.67532. × 1600. (p. 53)

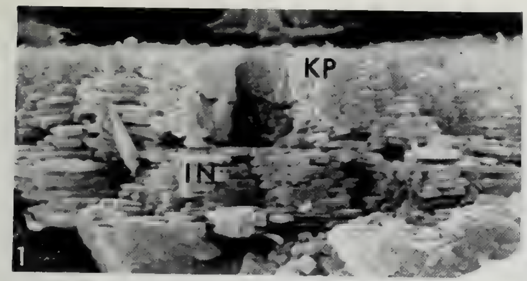
FIG. 3. Junction between main and inner shells marked by a parting between IP and KP ; middle of an interspace. C.67532. × 3250. (pp. 52, 57)

FIG. 4. Umbilical seam (U) of outer whorl (O) and its dorsal shell (D), overlying lateral part of venter of inner whorl (I) ; the dorsal shell consists only of the Nacreous Layer, for the Inner Nacreous Layer wedges out above the umbilical seam. Section at right angles to plane of coiling. C.67532. × 75. (p. 53)

FIG. 5. Corner of rib cavity, showing much recrystallized Outer Prismatic Layer (KP) of inner shell abutting against the Inner Prismatic Layer ; where the main and inner shells are in contact, KP is absent. C.77749. × 930. (p. 53)

FIG. 6. Earliest appearance of Inner Nacreous Layer below the Outer Prismatic Layer of the inner shell ; interspace. C.67532. × 3250. (p. 52)

FIG. 7. Enlargement of top right portion of Fig. 4, showing the Outer Prismatic and Nacreous Layers of the inner whorl, overlain by Nacreous Layer of dorsal shell of outer whorl. × 1500. (p. 53)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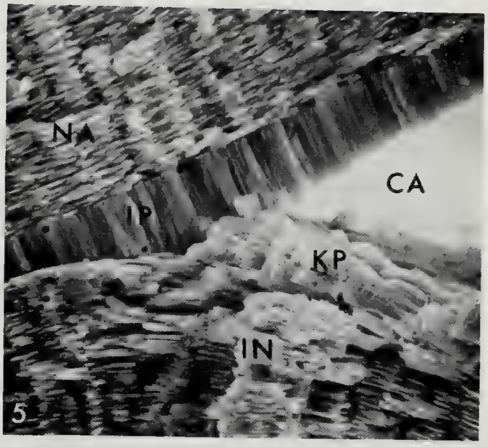
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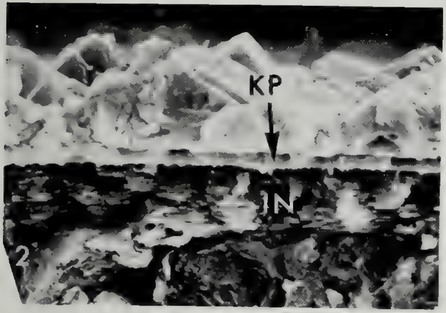
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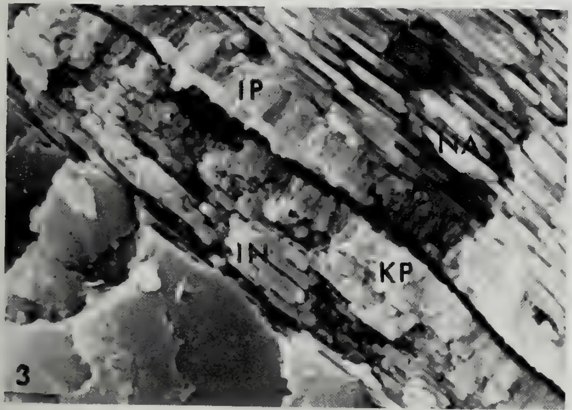
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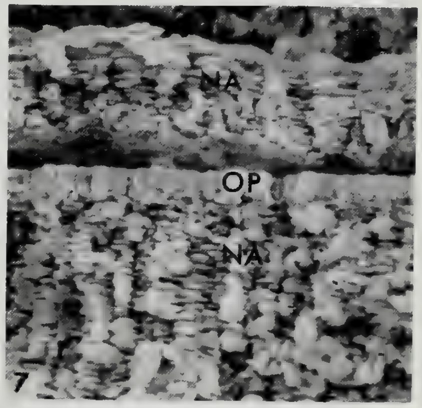
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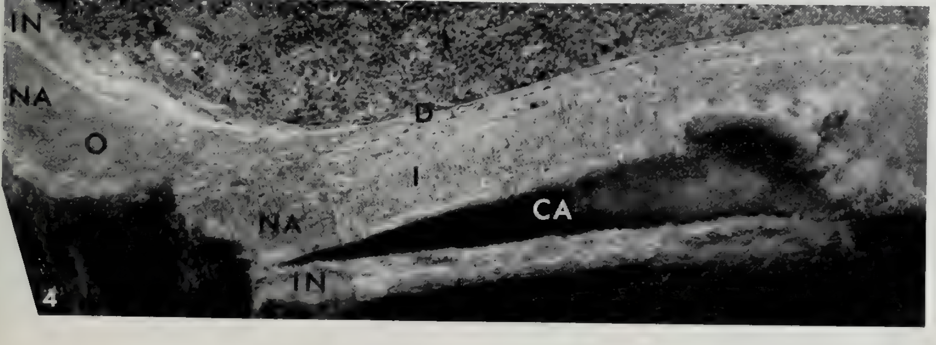
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PLATE 3

Zugodactylites braunianus (d'Orbigny)

Fig. 1. Outer Prismatic and Nacreous Layers of side of venter of inner whorl, overlain by Nacreous Layer and thick Septal Prismatic Layer forming dorsal shell of outer whorl. Section at right angles to plane of coiling. C.78545. × 1200. (pp. 53–4)

Peronoceras fibulatum (J. de C. Sowerby)

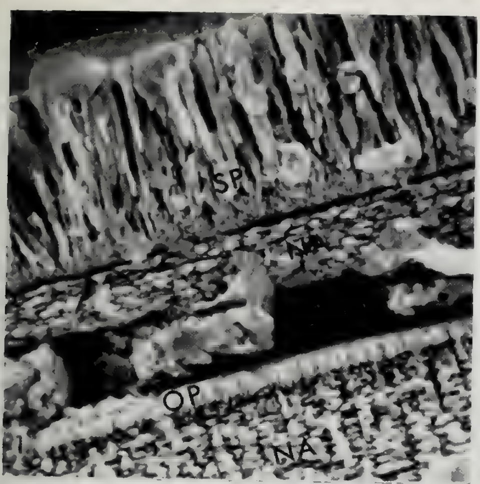
Fig. 2. Adult body chamber septum joining venter of previous whorl near crest of a rib ; adoral direction to left. See Text-fig. 1, p. 51. C.77749. × 70. (p. 55 ; see also Pl. 4, figs 1, 4 ; Pl. 5, fig. 3)

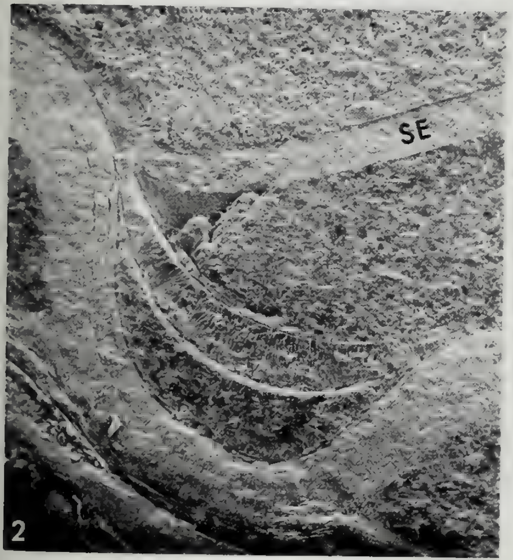
Fig. 3. Inner Nacreous and Septal Prismatic Layers on side of whorl about 5 mm adoral of final body chamber septum. C.77749. × 1350. (p. 54)

Fig. 4. Ribs 3 and 4 adoral to left-hand rib of Fig. 2, overlain by well-developed dorsal Septal Prismatic Layer of next outer whorl. C.77749. × 57. (p. 54)

Fig. 5. Enlarged portion of middle of Septal Prismatic Layer of Fig. 2. × 370. (p. 54)

Fig. 6. Crest of right-hand rib of Fig. 4 ; Outer Prismatic and Nacreous Layers of inner whorl overlain by dorsal Septal Prismatic Layer of outer whorl. × 1450. (p. 54)

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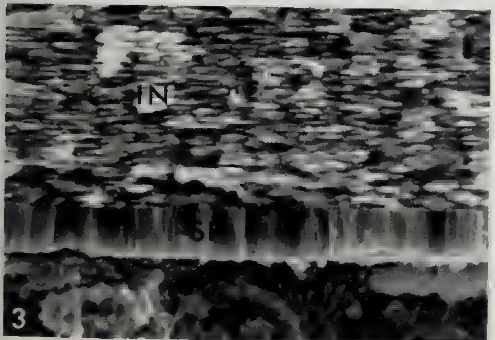
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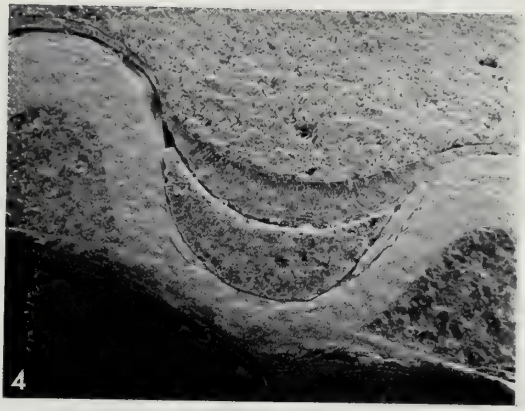
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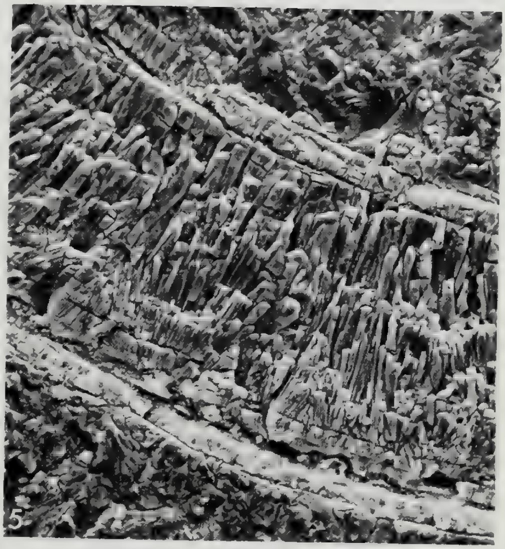
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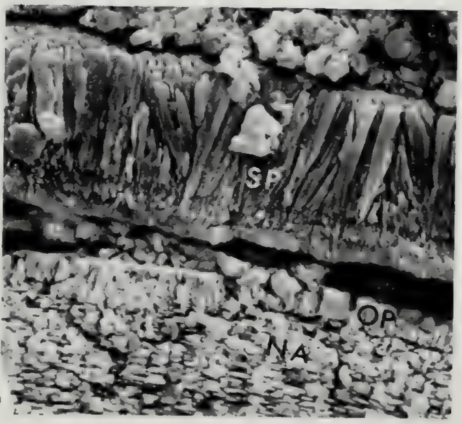
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PLATE 4

Peronoceras fibulatum (J. de C. Sowerby)

Fig. 1. Inner shell and Septal Prismatic Layer below the rib cavity in the left-hand rib of Pl. 3, fig. 2. C.77749. × 700. (p. 54)

Fig. 4. Enlargement of confluence between septum and dorsal Septal Prismatic Layer in Pl. 3, fig. 2, showing the change between prisms of the latter layer and nacre of the septum; half-way between centre of dorsum and umbilical seam. C.77749. × 350. (pp. 54, 59)

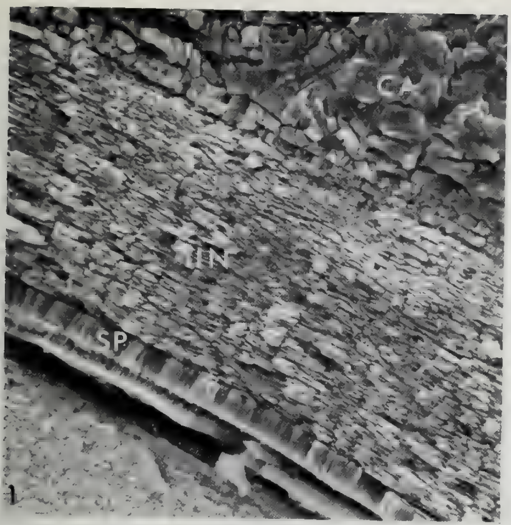
Zugodactylites braunianus (d'Orbigny)

Fig. 2. Lower part of whorl side 1–2 mm adoral of final septum; thick Septal Prismatic Layer attached to inside of Inner Nacreous Layer. C.78545. × 600. (p. 54)

Fig. 3. Middle of venter; Septal Prismatic Layer below Inner Nacreous Layer, 6 mm in front of final septum. C.78545. × 700. (p. 54)

Fig. 5. Confluence between septum and Septal Prismatic Layer below middle of venter. C.78545. × 650. (pp. 54, 59)

Fig. 6. Confluence between septum and Septal Prismatic Layer, overlying Outer Prismatic and Nacreous Layers of venter of inner whorl; section at right angles to plane of coiling. C.78545. × 250. (pp. 54–5, 59)



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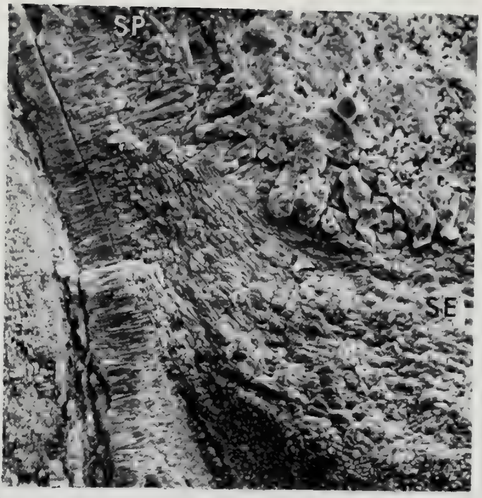

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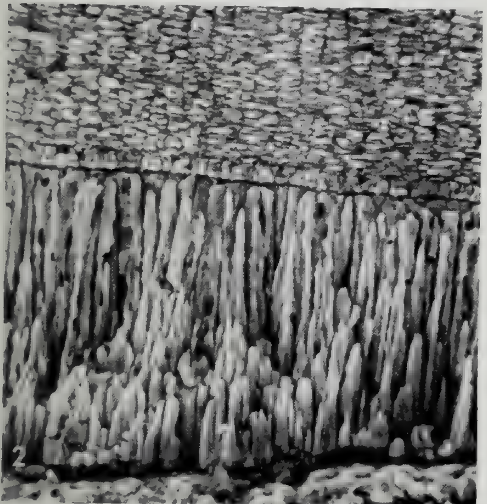

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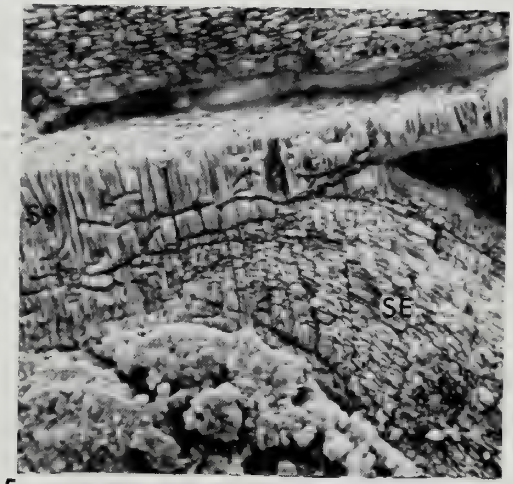

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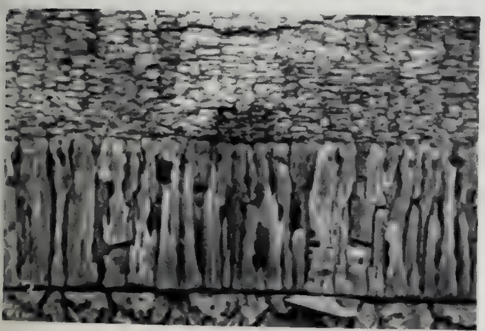

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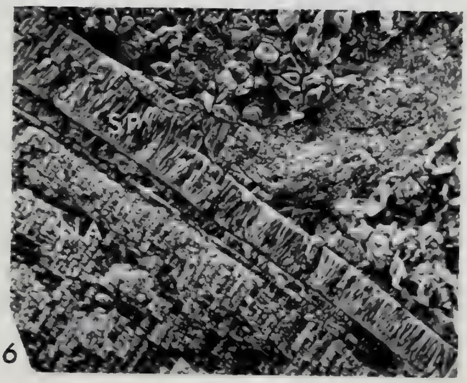

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PLATE 5

Peronoceras fibulatum (J. de C. Sowerby)

FIG. 1. Confluence between septum and Septal Prismatic Layer, showing rapid change of nacre into long prisms which form a humped mass ; this part of the Septal Prismatic Layer overlies a thin smooth layer (see Figs 4, 5), which is on top of an earlier part of the Septal Prismatic Layer that passes over the crest of a rib (to the left) on the venter of the inner whorl ; same septum as in Pl. 4, fig. 4, but in centre of the dorsum ; adoral direction to lower right. C.77749. × 375. (p. 55)

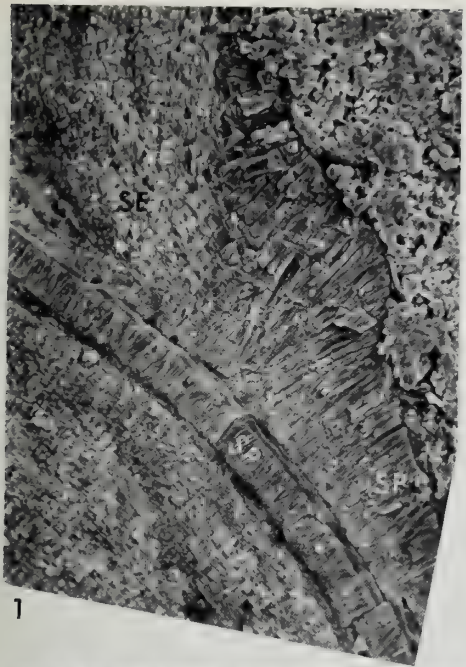
FIG. 2. Dorsal Septal Prismatic Layer between two ribs of venter of previous whorl, with a large central cavity filled with iron pyrites and secondary calcite. C.78595. × 160. (p. 55)

FIG. 3. Enlargement of part of the septum in Pl. 3, fig. 2, showing the thin adoral layer of prismatic crystals. C.77749. × 700. (p. 55)

FIG. 4. Middle of the first interspace adoral of Fig. 1 ; main part of Septal Prismatic Layer, now thick, below, overlain by smooth layer with 'building block' structure, then thin Septal Prismatic Layer at top which is adoral continuation of the septum. C.77749. × 800. (p. 55)

FIG. 5. Crest of second rib adoral of Fig. 4 ; smooth layer on top of Septal Prismatic Layer has marked 'building block' structure ; upper Septal Prismatic Layer continuation of septum now absent. C.77749. × 1500. (p. 55)

FIG. 6. Protoconch wall just before mouth of protoconch, showing the first (above) and second (below) prismatic layers of the protoconch. C.78601. × 2300. (p. 56)



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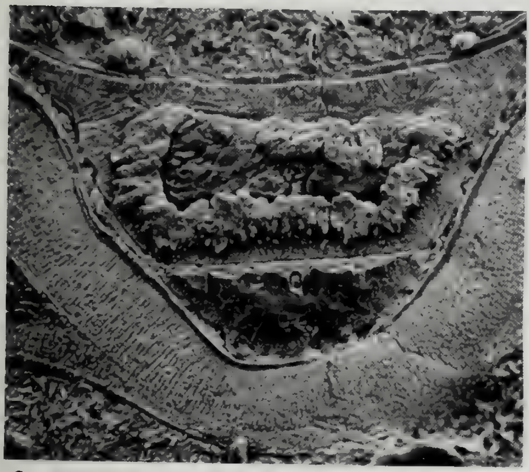

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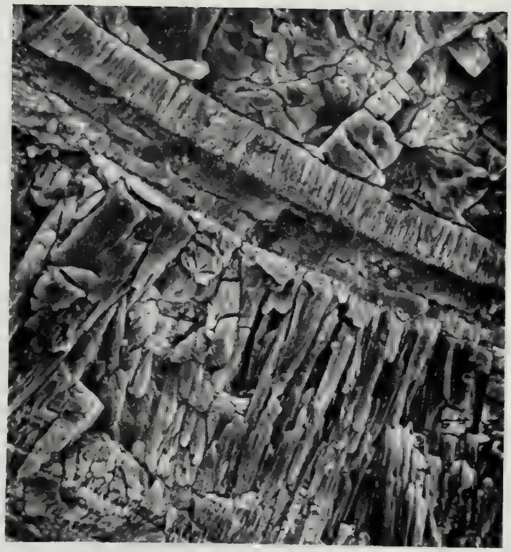

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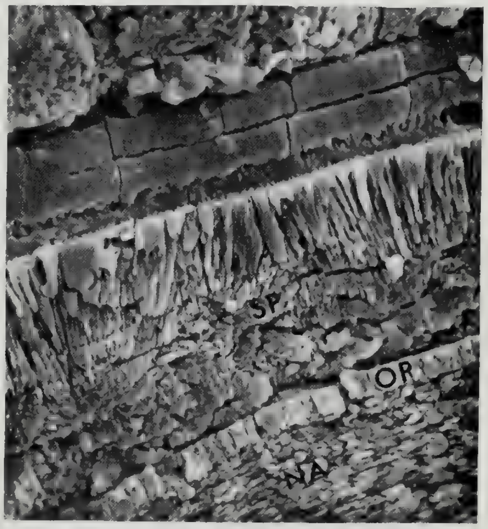

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PLATE 6

Peronoceras fibulatum (J. de C. Sowerby)

FIG. 1. Thick dorsal Septal Prismatic Layer between two ribs of venter of the previous whorl, with circular radiating masses of prisms in the upper half, and a small cavity near the centre filled with secondary calcite. C.78595. × 230. (p. 55)

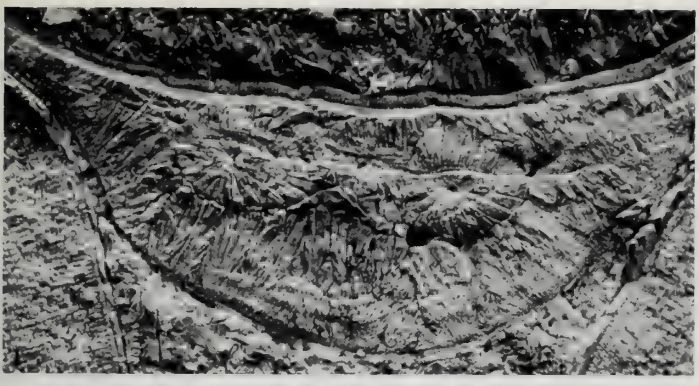
FIG. 2. Another part of the dorsal Septal Prismatic Layer of Fig. 1 ; shows an early portion attached to the outside of the inner whorl, truncated by a later portion which bridges across between the ribs ; the later part gives rise to part of a septum on the right. C.78595. × 230. (p. 55)

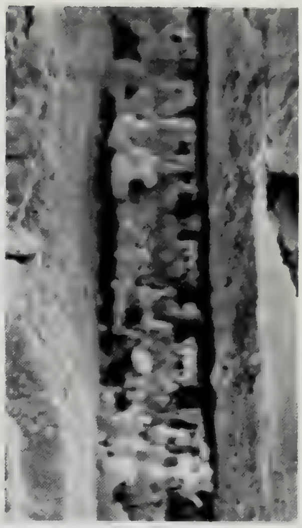
FIG. 3. Circular radiating masses of prismatic crystals formed in the cavity below the dorsal Septal Prismatic Layer. C.78594. × 800. (p. 55)

FIG. 4. Protoconch wall $\frac{3}{16}$ whorl after start ; single prismatic layer. C.78601. × 3600. (p. 56)

FIG. 5. Start of the first nacreous layer $\frac{3}{4}$ whorl after mouth of protoconch and immediately before the nepionic constriction ; a septum joins the inside (from the right) and spreads along the inner surface as a foot of prismatic crystals. C.78601. × 1000. (pp. 56, 59)

FIG. 6. Mid-ventral shell wall $\frac{9}{16}$ whorl after mouth of protoconch, consisting of a single prismatic layer (PL) ; a septum joins the dorsal Septal Prismatic Layer which is continuous over the outside of the whorl. C.78601. × 1000. (pp. 56, 59)





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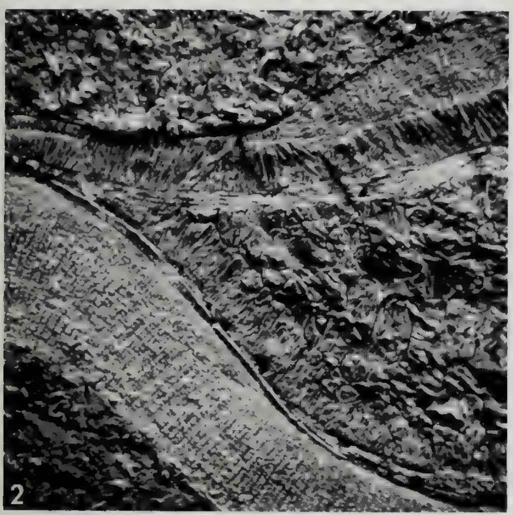

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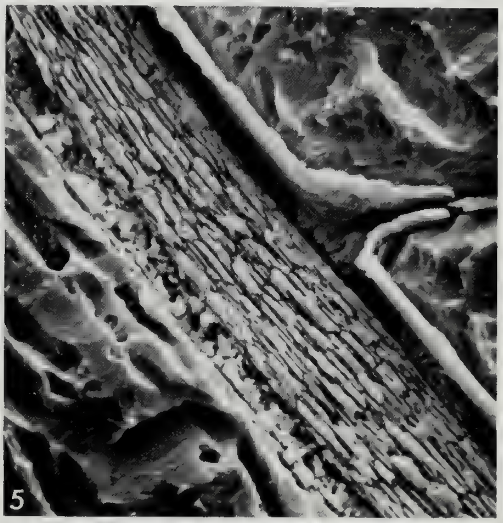

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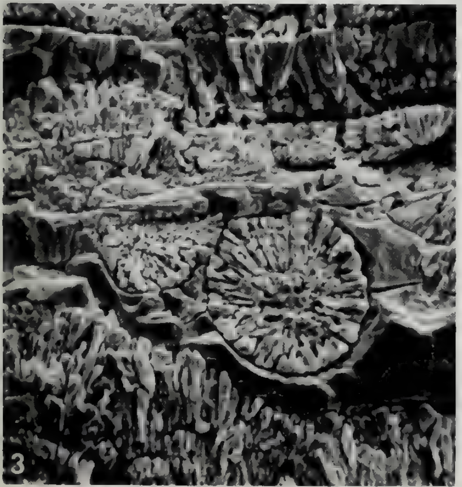

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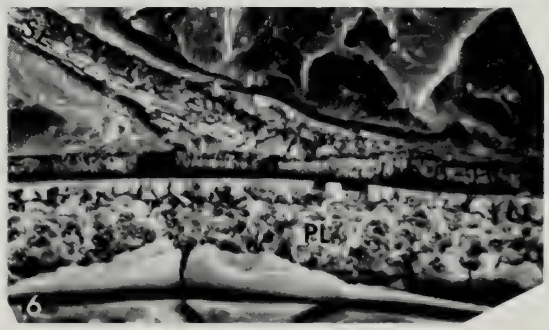

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PLATE 7

Peronoceras fibulatum (J. de C. Sowerby)

Fig. 1. Nepionic constriction, $\frac{13}{16}$ whorl after mouth of protoconch ; adoral direction to left ; a septum joins the inside from below, but is obscured between parallel sheets of calcite representing the conchiolin lining to both sides of the septum ; two septa of the next outer whorl join the outside from above, and are connected by the continuous dorsal Septal Prismatic Layer, which is deflected in places by defective preservation. C.78598. × 700. (pp. 56, 59)

Fig. 2. Mouth of protoconch, commencement of siphuncle (SI), caecum (C), prosiphon (P), proseptum and primary septum (both at X and close together in this median section), first nacreous septum (N) and two septa of the next outer whorl (S). C.78598. × 140. (pp. 56–7)

Fig. 3. Enlargement of part of Fig. 2, showing shell wall of first whorl, junction of first nacreous septum (N) with inside of venter, where there is no continuation of septum on inside of shell wall, and a septum (S) of the next outer whorl attached to a continuous dorsal Septal Prismatic Layer. × 1000. (pp. 56, 59)

Fig. 4. $1\frac{5}{16}$ whorls after protoconch ; septum joins inside of venter ; Inner Prismatic Layer not yet developed. C.78598. × 1000. (p. 59)

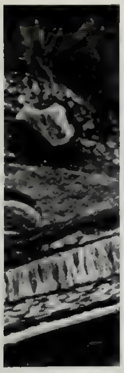
Fig. 5. $1\frac{5}{8}$ whorls after protoconch ; dorsal Septal Prismatic Layer of the next outer whorl is separated from outer surface of the Outer Prismatic Layer by a layer of secondary calcite. C.78601. × 1400. (pp. 57, 59)

Fig. 6. $2\frac{1}{4}$ whorls after protoconch. C.78601. × 750. (p. 57 ; see also Pl. 10, fig. 4)

Fig. 7. $1\frac{3}{8}$ whorls after protoconch. C.78601. × 1450. (p. 56)

Fig. 8. Immediately adoral of Fig. 7, showing start of Inner Prismatic Layer. × 1600. (p. 56)

Fig. 9. $1\frac{3}{4}$ whorls after protoconch. C.78601. × 700. (p. 57 ; see also Pl. 10, fig. 5)



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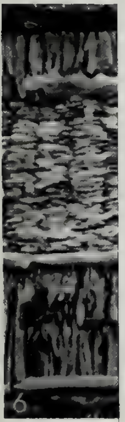

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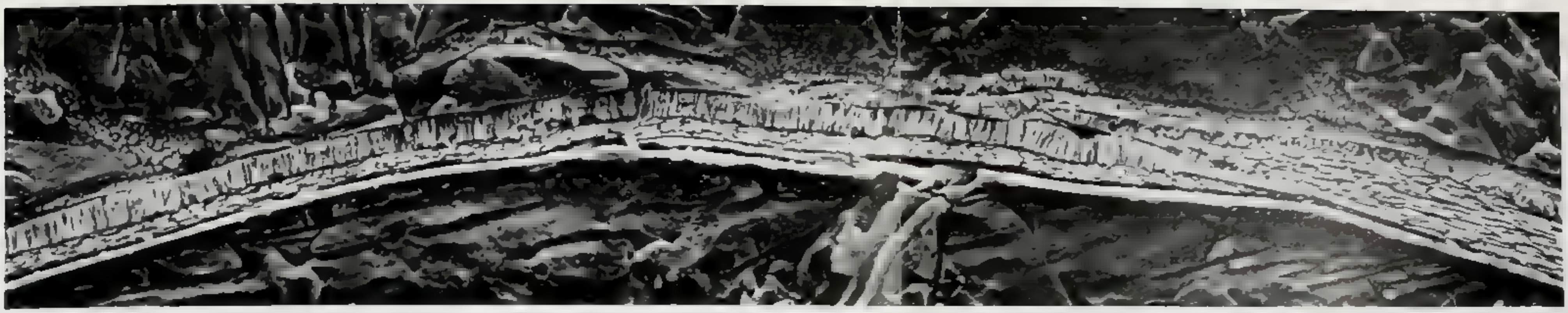

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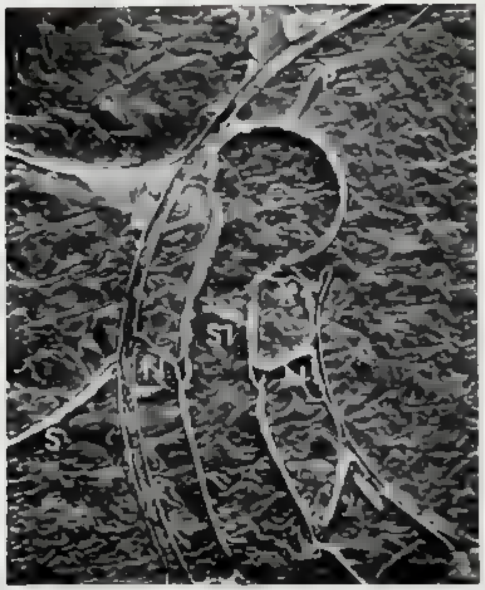

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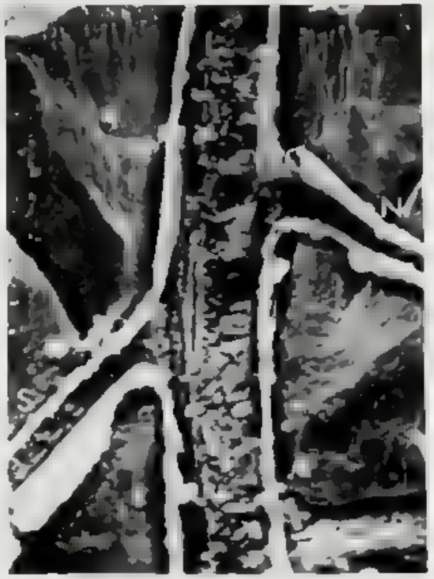

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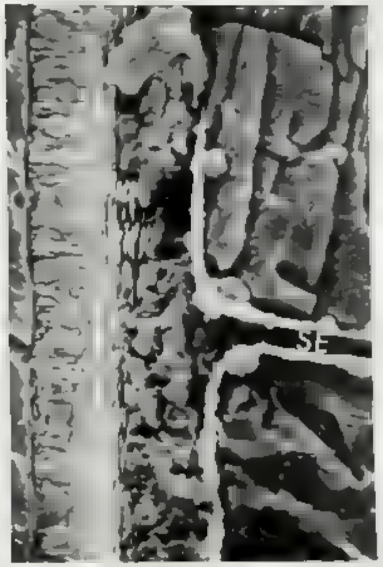

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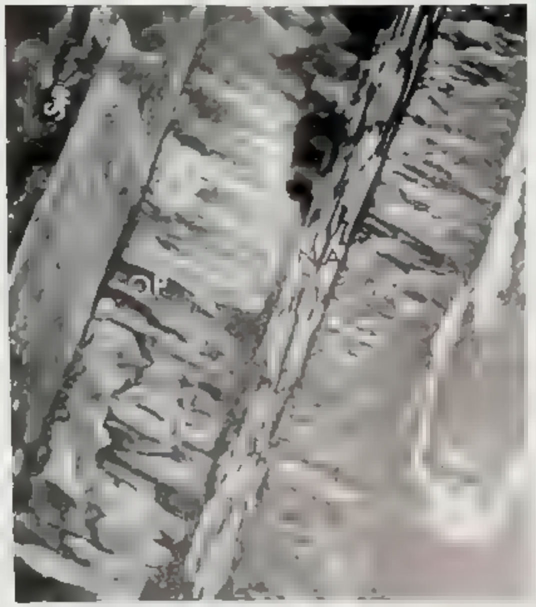

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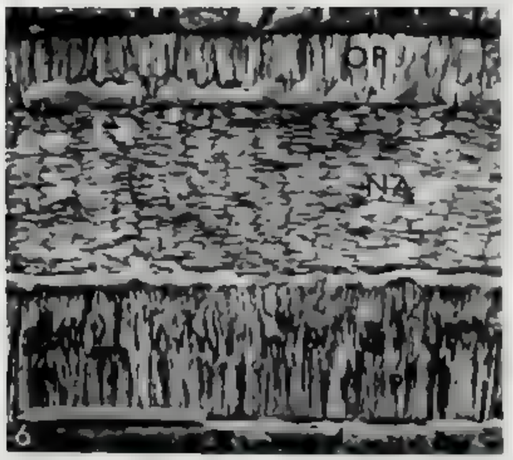

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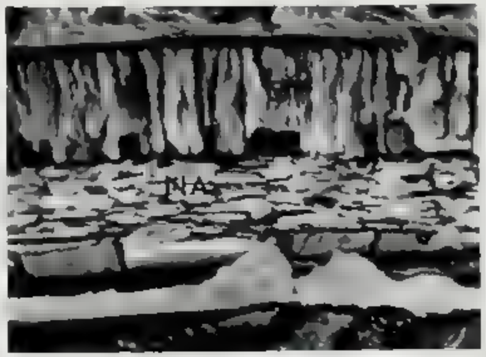

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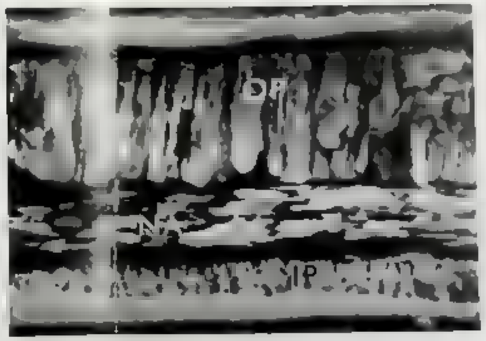

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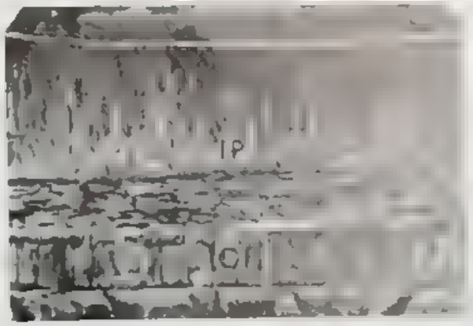

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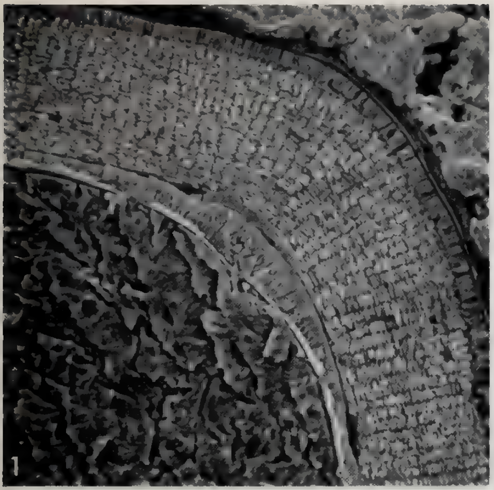

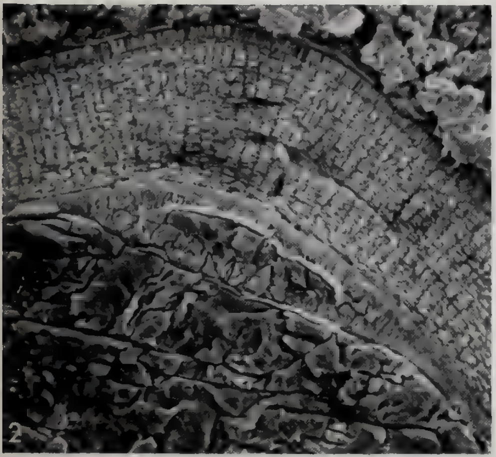

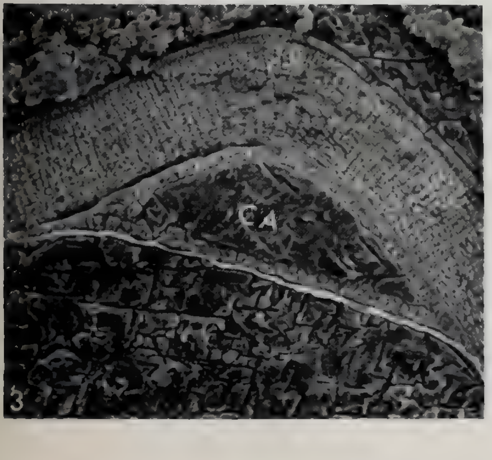

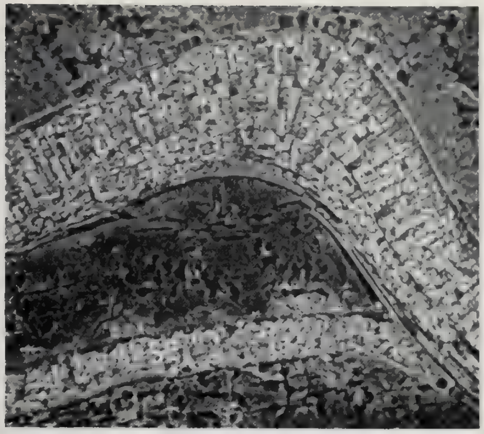
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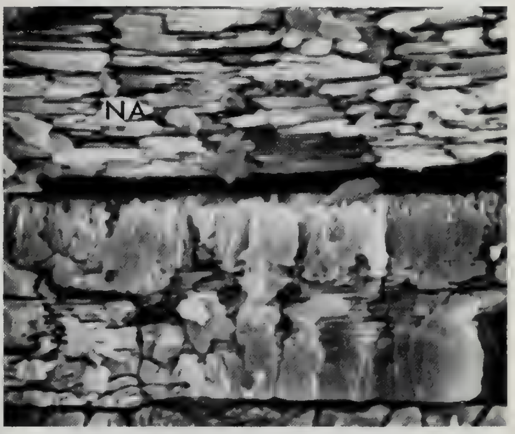

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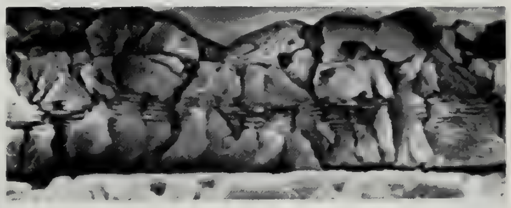
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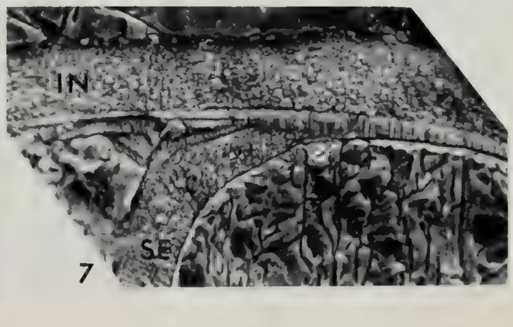

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PLATE 9

Peronoceras fibulatum (J. de C. Sowerby)

FIG. 1. Corner of a rib cavity with floor of cavity at top right, at a stage when the Inner Nacreous Layer is about equal in thickness to the Inner Prismatic and Septal Prismatic Layers ; eight ribs adoral to Pl. 8, fig. 3. C.78601. × 800. (p. 57)

FIG. 2. Corner of a rib cavity of the 13th rib (approx. $\frac{1}{4}$ whorl) adoral to Fig. 1 ; Inner Nacreous Layer now much thicker. C.78601. × 700. (p. 57)

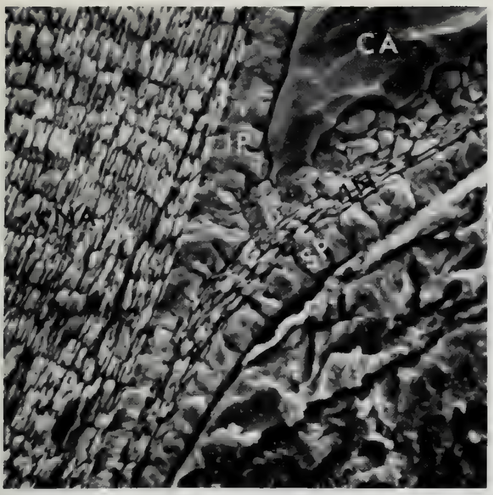
FIG. 3. Septum joined to ventral Septal Prismatic Layer below the inner shell, at a developmental stage between Figs 1 and 2 ; Inner Nacreous Layer somewhat disturbed by plates of secondary calcite. C.78598. × 650. (p. 57)

FIG. 4. Rib with well-developed cavity and inner shell, $\frac{1}{4}$ whorl adoral to Fig. 2, at whorl diameter of about 10 mm. C.78601. × 140. (p. 57)

FIG. 5. Near commencement of ventral ribs, seven ribs adapical of Pl. 8, fig. 1, with slight thickening of Inner Prismatic Layer on inside of the rib ; septum on left joins the inside with no continuity with the Inner Prismatic Layer ; septum on right is in next outer whorl and is continuous with the dorsal Septal Prismatic Layer. C.78601. × 375. (pp. 59–60)

Eleganticeras elegantulum (Young & Bird)

FIG. 6. Drift, *ex* Upper Lias, Falciferum Zone, Ahrensburg, Germany. Thick extra growth of Inner Prismatic Layer forms floor (F) that leaves cavity (C) in hollow keel ; specimen is detached from the inside of the Nacreous Layer which forms the bulk of the keel. Section at right angles to plane of coiling. C.67816. × 200. (p. 62)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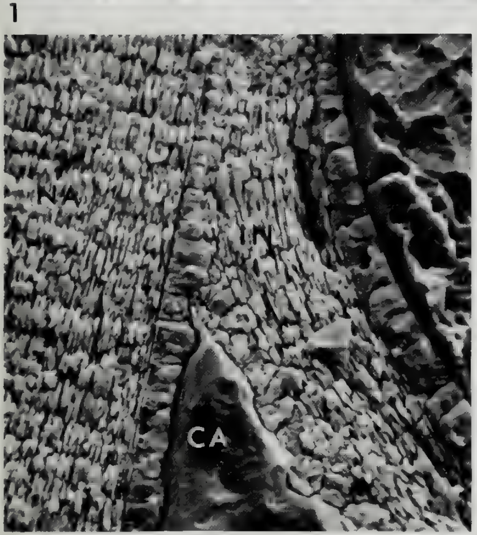

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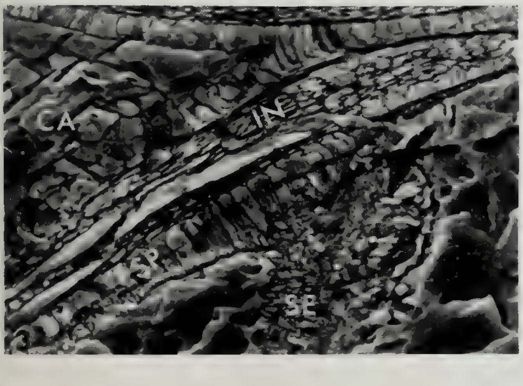

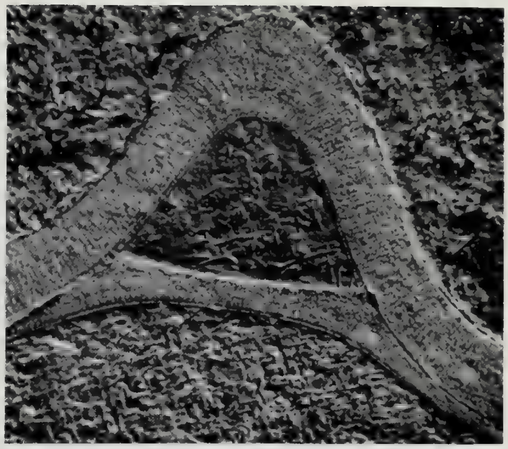

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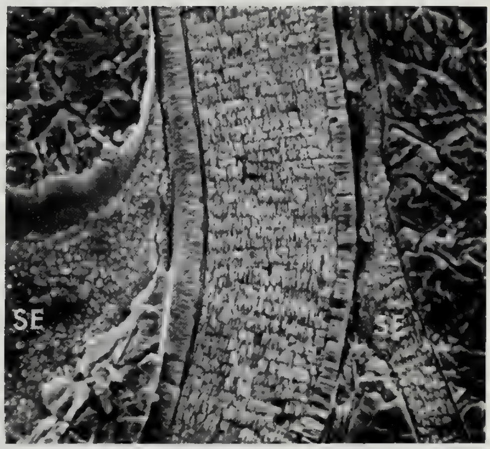

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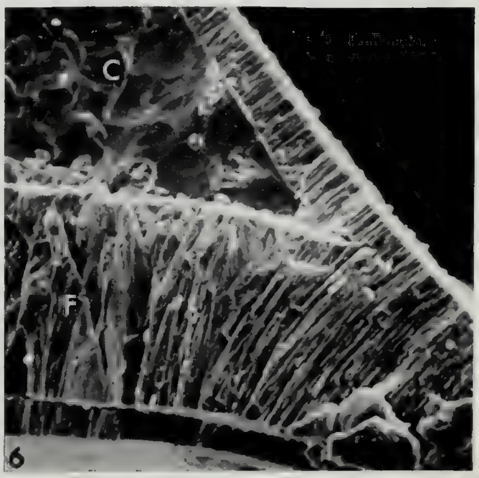


PLATE 10

Peronoceras fibulatum (J. de C. Sowerby)

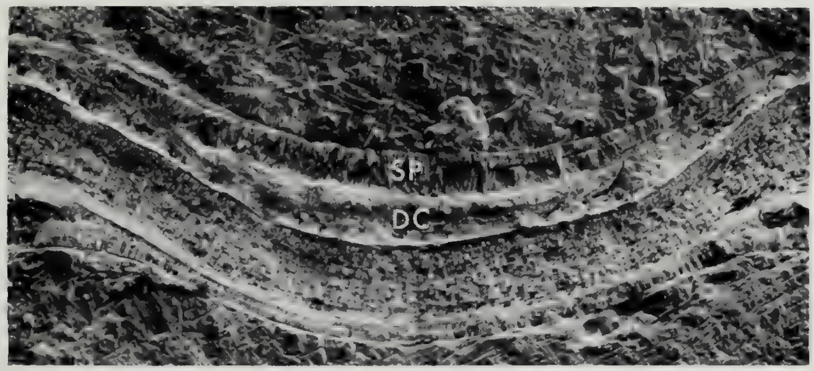
Fig. 1. Early formation of a cavity between the dorsal Septal Prismatic Layer and an interspace on the venter of the previous whorl ; the latter whorl is $3\frac{5}{8}$ whorls after the protoconch at whorl diameter of 8·5 mm. C.78594. × 175. (p. 60)

Fig. 2. Same specimen as Fig. 1 ; confluence between septum and Septal Prismatic Layer of the next outer whorl above the crest of a rib (Septal Prismatic Layer is detached from crest of the rib due to diagenetic changes). C.78594. × 530. (p. 60)

Fig. 3. Enlargement of part of the Septal Prismatic Layer in Fig. 1, with cavity below, then Outer Prismatic Layer and Nacreous Layer of part of the main shell of the inner whorl at the bottom. C.78594. × 600. (p. 60)

Fig. 4. Confluence between septum and inside of the Inner Prismatic Layer ; secondary calcite in lower corner separates Inner Prismatic Layer from the Nacreous Layer ; similar stage of development to Pl. 7, fig. 6. C.78601. × 1500. (p. 59)

Fig. 5. Septum and continuous dorsal Septal Prismatic Layer overlie outside of venter of inner whorl ; similar stage of development to Pl. 7, fig. 9. C.78601. × 750. (p. 60)



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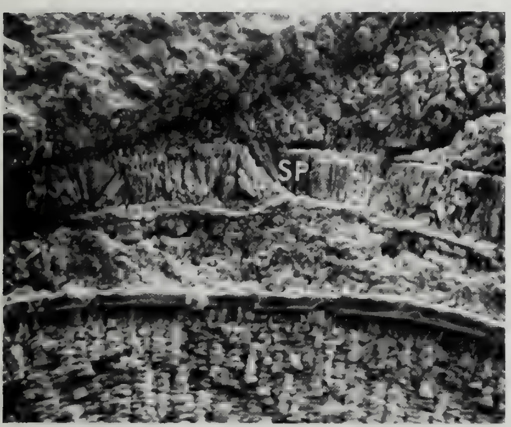

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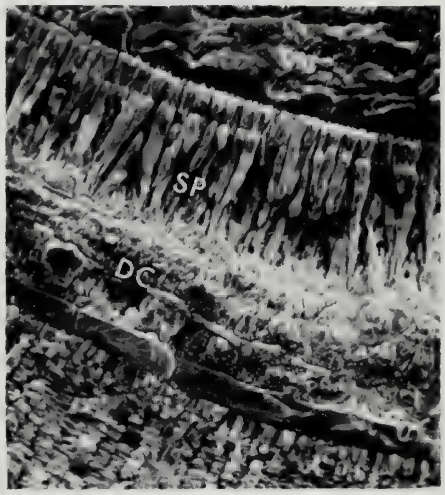

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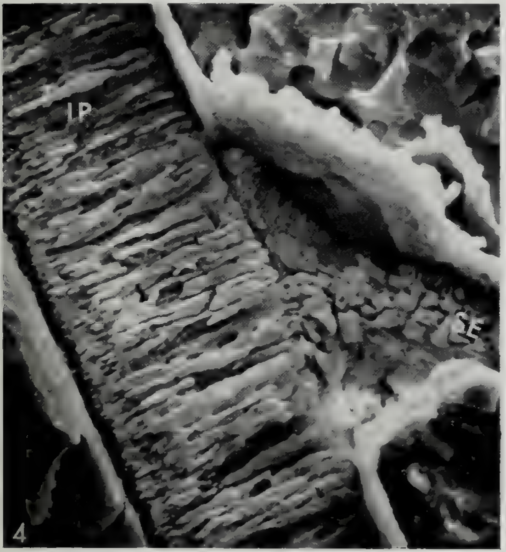

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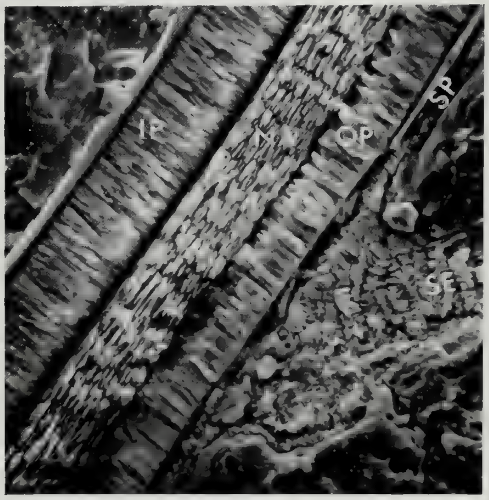

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P. H. GREENWOOD
AND
G. J. HOWES

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 26 No. 3
LONDON: 1975

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BY
PETER HUMPHRY GREENWOOD
AND
GORDON JON HOWES

Pp 69–127 ; 25 *Text-figures*

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NEOGENE FOSSIL FISHES FROM THE LAKE ALBERT–LAKE EDWARD RIFT (ZAIRE)

By P. H. GREENWOOD AND G. J. HOWES

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ABSTRACT

A large collection of fishes from Miocene, or possibly Pliocene, and Lower Pleistocene deposits in the Lake Albert-Lake Edward Rift (Zaire) is described and catalogued. Two new taxa are also described, a species of *Lates* (Centropomidae) showing several derived features in the syncranium, and a new genus and species of characoid fish whose affinities seem to be with American rather than African members of the suborder. This discovery has led to a reconsideration of the Egyptian fossil characoid *Alestes deserti* Greenwood.

Apart from these new taxa, the Miocene fish fauna of this area in the Western Rift Valley differs little from contemporaneous faunas in other parts of Africa, both north and south of the Sahara. The most noticeable difference, when comparisons are made with North African localities, is the absence of clariid and cyprinid fishes from Lower Miocene deposits in the Western Rift.

I. INTRODUCTION

THE MATERIAL which we have been privileged to study was collected principally by the Ganda-Congo expedition of 1960, and by Dr J. Lepersonne of the Musée Royal de l'Afrique Centrale on an earlier occasion, 1939–1940 (see Gautier 1970 for further details and references). Smaller collections by Dr X. Misonne (in 1958) and Dr J. de Heinzelin (in 1957) are also included.

Geographically, the sites cover the Lake Albert–Semliki–Lake Edward region (areas 5 and 6 in the map reproduced as fig. 1 in Gautier 1970), the northern region of the Semliki valley (area 3 in Gautier 1970) and an area near the southwestern shore of Lake Albert (areas 1 and 2 in Gautier 1970).

From the viewpoint of research on Quaternary fishes, this part of the Western Rift Valley is now undoubtedly the most intensively collected and studied region in all eastern Africa (Greenwood 1959). The new material extends our knowledge back to the Miocene, and substantially increases the information available on the Lower Pleistocene fish fauna of the area.

It is hardly necessary to stress the importance of a good palaeontological record when investigating the evolutionary history of the African lakes and their highly endemic fish faunas of today (Fryer & Iles 1972, Greenwood 1959, 1974a). Many earlier hypotheses put forward to explain this endemicity, the associated adaptive radiation of the fishes in each lake fauna, and their interrelationships with the faunas of other lakes, have been severely weakened by the later acquisition of good fossil records. Sadly, there is still a great dearth of such records for many of the lakes (especially Lakes Victoria, Tanganyika and Malawi). But, for the northern lakes of the Western Rift (Lakes Albert, Edward and George) the position is much better and a broad history of at least the non-cichlid fishes can be compiled for the Miocene to early Holocene periods (White 1926, Greenwood 1959, 1973a). Even for the cichlid fishes of these lakes the story is becoming clearer through evidence which can be derived from the history of the non-cichlids (Greenwood 1973a, 1974a, 1974b).

Probably the most important information derived from the fossils described in this paper concerns the Miocene fish fauna of the Albert–Edward Rift. Until now we were in complete ignorance of what this fauna might have been like. The answer is, in some respects, rather surprising. Besides what might be described as the 'expected' taxa there are two 'unexpected' elements. One is a species of the genus *Lates* (Centropomidae) showing superficial if not phyletic affinities with the endemic *Lates* species-group of Lake Tanganyika. The other is an undescribed characoid fish whose affinities are apparently closer to a lineage now confined to South America (the Serrasalminae) than to any lineage still extant in Africa. These new taxa are described and discussed below before we go on to give an annotated catalogue of all identifiable specimens obtained from the various sites.

All the material reported upon here is deposited in the Musée Royal de l'Afrique Centrale, Tervuren. Only type material is registered in this collection, with numbers lying in the range RG.17.501 to RG.17.600.

Abbreviations used in the text figures:

ADD R	Ridge for insertion of the *adductor mandibulae* I muscle	LC	Lateral commissure
ADD SP	Spur for insertion of the *adductor mandibulae* I muscle	N	Notch between ascending and articular processes
AHYF	Anterior facet for hyomandibula	OCS	Occipito-spinal nerve foramen
ART P	Articular process of the premaxilla	OPSORBC	Anterior opening of supra-orbital laterosensory canal
ASC P	Ascending process of the premaxilla	PAR	Parietal
BOC	Basioccipital	PHYF	Posterior facet for hyomandibula
BSP	Basisphenoid	PMAXP	Posterior maxillary process
Cl	Cleft between ascending and articular processes	PMXP	Premaxillary process of the maxilla
D PROC	Dorsal process of the maxilla	PRO	Prootic
E	Mesethmoid	PS	Parasphenoid
EPI	Epiotic	PSGR	Groove in parasphenoid
EXO	Exoccipital	PTO	Pterotic
F	Foramen in articular process	PTF	Post-temporal fossa
FR	Frontal	PTS	Pterosphenoid
FRR	Frontal ridge	RA	Retroarticular
GR	Groove	SPO	Autosphenotic
IC	Intercalar	V	Vomer
LATE	Lateral ethmoid	VS	Vomerine spine
LATSGR	Laterosensory canal groove	IX	Foramen for glossopharyngeal nerve
LAT SP	Pores to laterosensory canal	X	Foramen for vagus nerve

II. NEW SPECIES OF FISH FROM THE MIOCENE AND EARLY PLEISTOCENE OF THE LAKE ALBERT–LAKE EDWARD RIFT

Superorder ACANTHOPTERYGII

Order PERCIFORMES

Family **CENTROPOMIDAE**

Lates rhachirhinchus sp. nov.

(Figs 1–21)

Material and locality. The material on which this new taxon is based comprises numerous but invariably incomplete and often fragmentary bones from the syncranium and vertebral column. It was obtained from sites situated within an area of about 1·5 km^2 in the Sinda-Mohari region of the lower Semliki valley (Hooijer *et al.* 1963 : fig. 5). The principal sites are in the basal Sinda Beds at Ongoliba (collected by X. Misonne) and at Sinda-Mohari, points 1, 2 and 10 of the Ganda-Congo expedition, 1960 (Gautier 1965, 1970). (Additional specimens which were not used in this description, except indirectly to check various characters, are listed in the review of sites on pp. 106–119).

Age. There is some uncertainty about the precise age of the basal Sinda Beds, from which the majority of *L. rhachirhinchus* remains were recovered (Gautier 1970 : 69–76). Published evidence suggests an uppermost Pliocene or early Pleistocene (Lower Villafranchian) age (Gautier 1970 : 73). However, preliminary unpublished results stemming from a revision of the mammalian fauna indicate the possibility of an early Pliocene dating (Dr J. Lepersonne *in litt.*, referring to the work of Dr C. T. Madden, University of Michigan).

Holotype. A vomer (Fig. 6A) with an almost complete spine ; from Sinda-Mohari Point 10 (Ongoliba Bone Beds, base of Sinda Beds – earlier Pleistocene ; see p. 112) (Hooijer 1970, Lepersonne 1970). RG.17.501.

Paratypes. (The sites are given in brackets, after a brief description of each specimen) :

Neurocranial material

1. Occipital region of skull, extending from the anterior margin of the prootic to the basioccipital facet ; 11 cm long ; (basal Sinda Bone Beds, Ridge 1). RG.17.502.
2. Damaged occipital and posterior orbital region of skull ; (basal Sinda Bone Beds, Ridge 1). RG.17.503.
3. Specimen similar to above, but rather distorted ; (basal Sinda Bone Beds, Ridge 1). RG.17.504.
4. Incomplete occiput from a smaller fish than those previously listed ; (basal Sinda Bone Beds, Ridge 1). RG.17.505.
5. Incomplete otico-occipital region, slightly compressed ; (basal Sinda Bone Beds, Ridge 1). RG.17.506.
6. Otico-occipital region, not distorted, and comprising about the same region of the skull as specimen 1 ; (basal Sinda Bone Beds, Ridge 1). RG.17.507.

7. Otico-occipital region of the skull from a large fish, rather damaged; (basal Sinda Bone Beds, Sinda-Mohari, point 10). RG.17.524.
8. Fragment of neurocranium, comprising part of the otic region, with roofing bones but no parasphenoid; (basal Sinda Bone Beds, Sinda-Mohari, point 10). RG.17.508.
9. Almost complete skull, although damaged and compressed in places; (Ongoliba bone bed, basal Sinda). RG.17.509.
10. Vomer; 3 specimens in which the tooth patch is 18 mm (f1) or 19 mm (f2) across; (basal Sinda Bone Beds, Sinda-Mohari, point 2). RG.17.510–512.
11. Vomer; 11 specimens, variously damaged; width of tooth patch on largest specimen *c* 25 mm, and *c* 13 mm on the smallest; (basal Sinda Bone Beds, Sinda-Mohari, point 10). RG.17.513–523.
12. Anterior part of the dorsicranium, together with the ethmoid region; (basal Sinda Bone Beds, Sinda-Mohari, Ridge 1). RG.17.525.

Jaws, Palatoquadrate arch, etc.

13. Premaxillae; 14 specimens, variously damaged, 6 left and 8 right; (basal Sinda Bone Beds, Sinda-Mohari, point 10). RG.17.526–539.
14. Dentary; almost complete left ramus (length from symphysis to angle between ascending and horizontal arms 114 mm); (basal Sinda Bone Beds, Sinda-Mohari, point 1, ridge 1). RG.17.540.
15. Dentary; 27 fragmentary specimens; (basal Sinda Bone Beds, Sinda-Mohari, point 10). RG.17.541–567.
16. Quadrate; 2 fragments, comprising the articulatory surface; (basal Sinda Bone Beds, Sinda-Mohari, point 10). RG.17.568–569.
17. Quadrate; somewhat damaged but comprising the articulatory surface and part of the body; (basal Sinda Bone Beds, Sinda-Mohari, point 10). RG.17.570.
18. Quadrate; damaged, right; (basal Sinda Bone Beds, Sinda-Mohari, point 2). RG.17.571.
19. Premaxillae, one left, one right; (basal Sinda Bone Beds, Sinda-Mohari, point 10). RG.17.572.
20. Dentary; about the anterior half of left ramus; (basal Sinda Bone Beds, Sinda-Mohari, point 2). RG.17.573.
21. Premaxillae; one left, one right; (Karugamania, Lower Miocene; coll. J. de Heinzelin). RG.17.574.
22. Maxillae; 3 (1 left, 2 right), variously damaged; (basal Sinda Bone Beds, Sinda-Mohari, point 10). RG.17.575–577.
23. Angulo-articular; 12 damaged specimens; (basal Sinda Bone Beds, Sinda-Mohari, point 10). RG.17.578–589.
24. Angulo-articular; one right, from skull about 18 cm long; (basal Sinda Bone Beds, Ridge 1, basin B). RG.17.590.
25. Angulo-articular with attached retroarticular, right; (Ongoliba Bone Bed, basal Sinda). RG.17.591.
26. Autopalatine, left, anterior part only; (basal Sinda Bone Beds, Sinda-Mohari, point 10). RG.17.592.

27. Autopalatine, right ; the anterior region but with a small part of the associated tooth-bearing dermopalatine ; (basal Sinda Bone Beds, Sinda-Mohari, point 5). RG.17.593.

Vertebrae

28. First abdominal ; width of anterior face 25·5 mm, of posterior face 30·5 mm ; (basal Sinda Bone Beds, Sinda-Mohari, point 10). RG.17.594.
29. Third abdominal ; width of anterior face 39·0 mm, of posterior face 42·0 mm ; (basal Sinda Bone Beds, Ridge 1). RG.17.595.
30. ? Fourth–fifth abdominal ; width of anterior face 24·0 mm, of posterior face 26·0 mm ; (basal Sinda Bone Beds, Sinda-Mohari, point 10). RG.17.596.
31. Posterior abdominal (position indeterminable) ; width of anterior face 47·0 mm, least width of centrum 40·0 mm ; (basal Sinda Bone Bed, point 10). RG.17.597.
32. Caudal (position indeterminable) ; width of anterior face 13·5 mm, width of posterior face 13·0 mm, length of centrum 16·0 mm, least width of centrum 8·0 mm ; (basal Sinda Bone Bed, Sinda-Mohari, point 10). RG.17.598.

ETYMOLOGY. The specific name *rhachirhinchus* is derived from the Greek *ῥάχις* a spine, and *ῥῖνες* a snout. It refers to the peculiar spine-like process on the vomer (p. 83).

SIZE RANGE. It is difficult to estimate from such fragmentary material the size of the fishes represented. Basing our estimates on the size of certain neurocranial bones and on the dimensions of vertebral centra as compared with similar bones in the skeleton of extant *Lates niloticus* and *L. calcarifer*, the size range of the *L. rhachirhinchus* represented is from *c* 30 to *c* 200 cm standard length.

DIAGNOSIS. *Lates rhachirhinchus* differs from all living species of the genus principally in having a forwardly projecting median spine on the vomer (p. 83) ; by peculiarities in the shape of the premaxilla, maxilla and articular (pp. 86, 85, 88 respectively) ; in having a narrow and ventrally convex parasphenoid with a deep median groove on its posterior third (p. 82), a shallow post-temporal fossa that does not open into the cranial cavity (p. 77), a broad lateral commissure (p. 80), frontal ridges that extend far anteriorly and then fuse medially (p. 77) ; by differences in the shape of the autopalatine (p. 85) ; and by several differences in the morphology of the first and third to seventh abdominal vertebrae (pp. 81–85). Other differential characters are discussed below.

Where these features can be compared with their counterparts in other fossil *Lates*, they are also diagnostic (see review of fossil *Lates* species by Sorbini 1973). An exception is provided by the palatine of *L. rhachirhinchus*, which is virtually identical with a palatine from the Pliocene deposits of Wadi Natrun, Egypt (p. 85 ; Greenwood 1972). The other *Lates* material from Wadi Natrun, however, shows typical *L. niloticus*-like characteristics.

NEUROCRANIUM. Judged on the abundant though incomplete skull material, the neurocranium of *L. rhachirhinchus* is narrower than that of any extant African centropomid, especially in the preorbital and interorbital regions and in the posterior otic region. It also has a lower vault, and lower, but stouter and anteriorly more extensive, fronto-parietal ridges. Other unique features are the vomerine spine, the poorly developed post-temporal fossa and the relatively more elongate otico-occipital region.

Narrowing of the preorbital skull, and especially of the lateral ethmoids, has apparently led to the loss of a foramen for the olfactory nerve and blood vessel in these bones. This feature, together with the vomerine spine and the imperforate post-temporal fossa, is unique within the genus and, apparently, within the Centropomidae as a whole. All must be ranked as derived, i.e. apomorph, features.

In the detailed description below, all comparisons with extant species of *Lates* should be taken to include comparison with the monotypic genus *Luciolates stappersi* whose neurocranial architecture is essentially like that of *Lates*.

DORSICRANIUM. The skull roof is narrow, the width across its otic region being only a little greater (about 1½ times) than at the exoccipital condyles. Expressed in another way, the maximum breadth of an entire *L. niloticus* skull 12·5 cm long is about equal to that of an incomplete fossil neurocranium measuring 11 cm from the basioccipital facet to the anterior point of the prootic.

The frontals and parietals have prominent and robust crests, those of the frontals extending forward to a point level with the anterior opening of the supraorbital lateral-line canal, i.e. almost to the posterior part of the ethmofrontal suture. Over the anterior part of their course the frontal ridges of each side are at first parallel to one another, but then become closely apposed. Shortly after that point the ridges fuse and disappear (Fig. 1 ; cf. Fig. 5A, B).

The first opening to the supraorbital lateral-line canal is large and lies in a deep gutter. Somewhat posteriorly is another opening to this canal lying in a high and ʌ-shaped coaming of bone that extends antero-laterally at an angle to the frontal ridge with which it merges medially (Fig. 5).

Judged on the only specimen in which the frontals roofing the orbit are preserved (p. 000), the fossil has extremely narrow preorbital and interorbital regions, narrower even than in *Luciolates*. This narrowness is partly due to the narrow frontals but also results from the lateral ethmoids not being laterally expanded.

In no specimen is the supraoccipital crest complete, so its height cannot be determined. However, in two specimens the bone's anterior extension is probably determinable. In one specimen it seems not to extend forward beyond a point level with the middle of the sphenotic ; in the other it reaches a point level with the midpoint of the hyomandibular facet in the pterotic. All extant *Lates* species have the supraoccipital extending forward beyond these points (Fig. 1A) ; it is least extensive in *L. calcarifer*.

The post-temporal fossa is a shallow, rather elongate depression with a complete bony floor (Fig. 4). In this respect *L. rhachirhinchus* contrasts strongly with all extant *Lates* species. In these taxa the fossa is a clearly circumscribed and deep cavity with a medioventral opening into the brain case, closed in life by a tough membrane. Even in *Luciolates*, where the fossa is shallower than in *Lates*, it is perforate and far more definite than in *L. rhachirhinchus*.

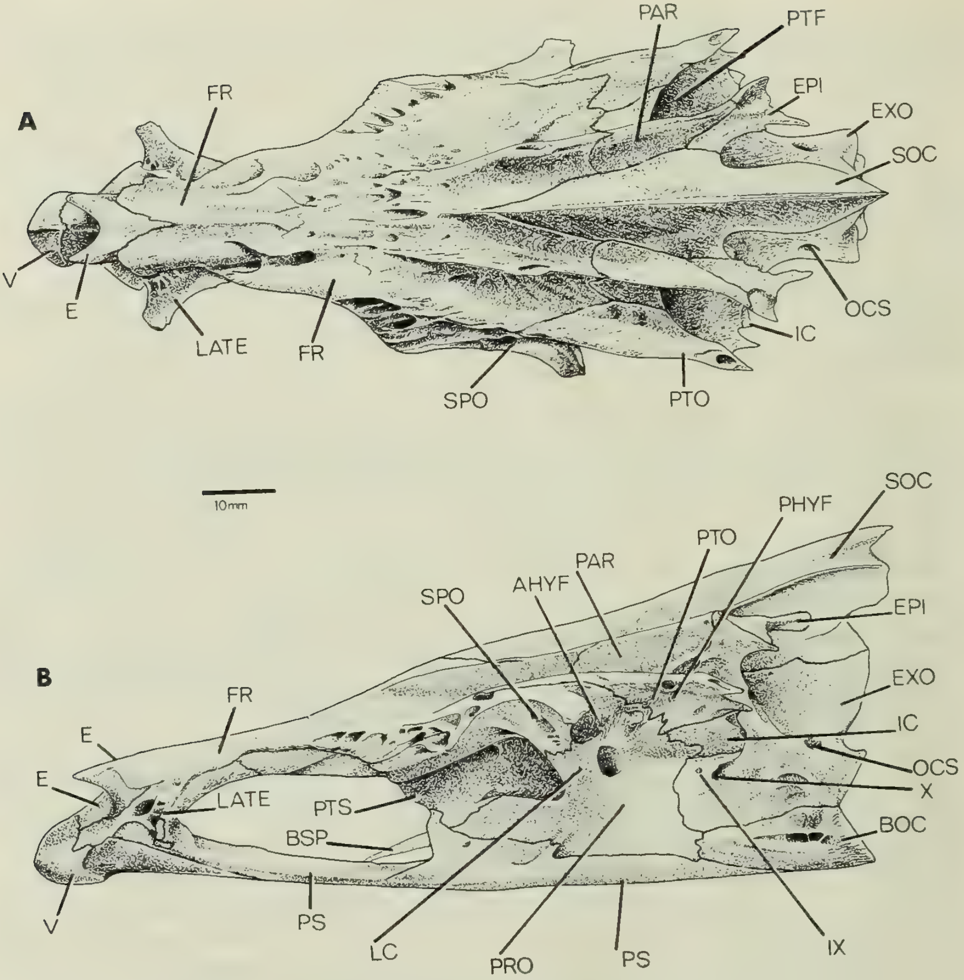
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FIG. 1. *Lates niloticus*. Neurocranium. A. Dorsal view. B. Left lateral view.

All lateral line canals on the skull roof are bone-enclosed.

ORBITAL, OTIC AND OCCIPITAL SKULL REGIONS. The pterosphenoid is an expansive bone extending forward into the orbit and coming into broad and close contact ventrally with the prootic (Figs 2, 3). Unfortunately in no specimen is it possible to see clearly the exact relationships between the prootic, pterosphenoid and parasphenoid. In extant species there are clear-cut interspecific and ontogenetic differences in this posterior region of the orbit. Some species (e.g. *Lates calcarifer*, *L. niloticus*, *L. angustifrons*) have a distinct pterosphenoid pedicle which provides a tunnel for the oculomotor and profundus nerves, and the internal jugular vein. Others, including *Luciolates*, have no pedicular tunnel, the nerves and blood vessel being bridged only by a narrow ligamentous or osseous arch (Greenwood, unpublished). Correlated with this latter condition, the pterosphenoid is relatively foreshortened and not expansive as it is in *L. rhachirhinchus* and those species with a pedicular tunnel. However, an expansive pterosphenoid does not necessarily imply the development of a tunnel and thus it cannot be concluded that one existed in *L. rhachirhinchus*.

In *L. rhachirhinchus*, unlike any extant *Lates* species, the ascending parasphenoid wing, which meets the prootic, rises in a gentle slope, not a pronounced step, and there is a corresponding antero-ventral prolongation of the prootic (Fig. 2A). Also unlike the condition in living species is the relatively acute angle formed by the sphenotic and prootic bones where they meet, lateral to the anterior opening of the trigemino-facialis chamber (Fig. 2A).

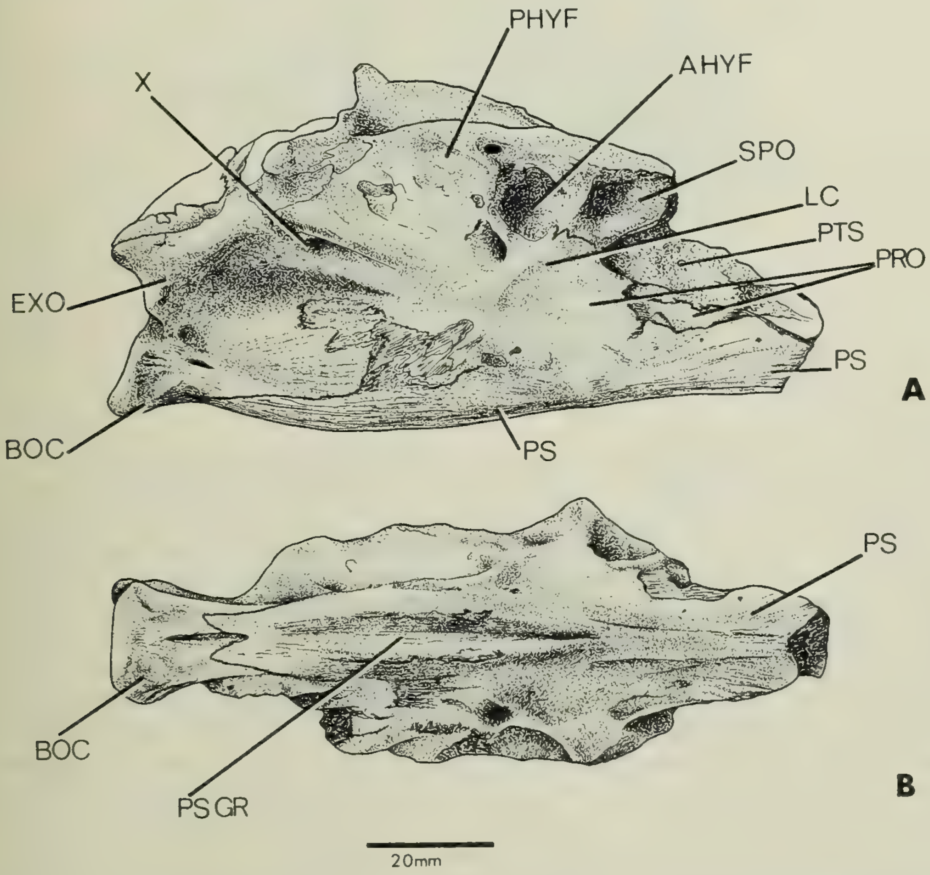

FIG. 2. *Lates rhachirhinchus*. Otico-occipital region of the skull. A. Right lateral aspect. B. Ventral view. (Paratype RG.17.502.) Unstippled areas represent adherent matrix.

The sphenotic, immediately anterior and dorsal to its suture with the prootic, is deeply excavated so as almost to mirror the anterior hyomandibular facet (Figs 2, 3). In all other respects the sphenotic does not differ greatly from the condition found in living species.

The prootic, in its general outline, does not depart markedly from that bone in other *Lates* species, but see above with regard to its contact with the parasphenoid. The lateral commissure, however, is relatively much wider in *L. rhachirhinchus*, and the openings to the trigemino-facialis chamber are apparently larger (Figs 2, 3).

Both the anterior and posterior cranial facets for the hyomandibula are well-defined, the anterior one (in the prootic and sphenotic) is a deep, hemispherical pit, the posterior one a relatively shallow and elongate groove on the pterotic.

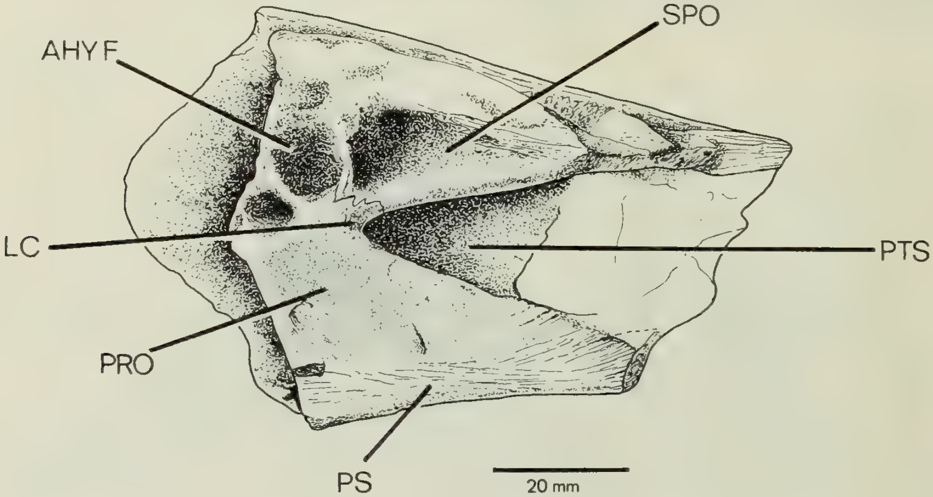

FIG. 3. *Lates rhachirhinchus*. Otico-occipital region of the skull in right lateral view. (Paratype RG.17.507.) Unstippled areas represent adherent matrix.

Compared with most extant species, the otic region in *L. rhachirhinchus* is narrower and shows none of the slight inflation generally characterizing the anterior and ventral regions of this part of the skull ; in this respect *L. rhachirhinchus* resembles *Luciolates* and *L. angustifrons* rather more closely.

A deep groove on the exoccipital runs obliquely antero-ventrally, from the large vagus and smaller glossopharyngeal nerve foramina (Fig. 4). Below this groove the area of the exoccipital bordered ventrally by the suture with the basioccipital, and posteriorly by the buttress of the facet, is concave like the same area in extant species. The exoccipital facets are apparently circular in outline (kidney-shaped in other species), but each has a medially directed, tab-like projection that meets its counterpart in the midline below the foramen magnum. A large nerve foramen penetrates the upper surface of the prominent buttress leading to the facet (Fig. 2A).

The basioccipital has the same proportions and morphology as in all extant species, although the facets for Baudelot's ligament seem somewhat deeper. When

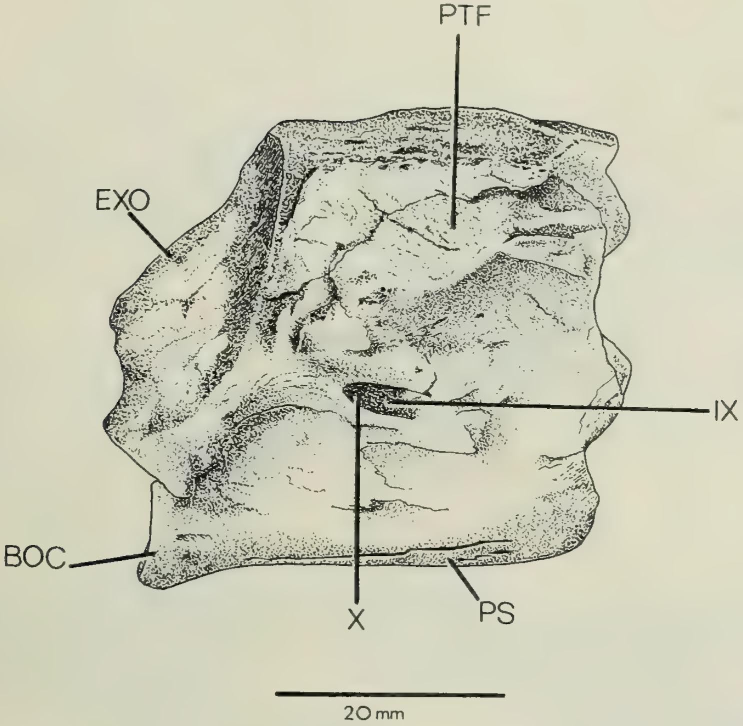

FIG. 4. *Lates rhachirhinchus*. Occipital region of the skull, in right lateral view, to show the complete bony floor to the post-temporal fossa. (Paratype RG.17.506.)

the skull is viewed laterally the ventral surface of the basioccipital and underlying parasphenoid slopes gently but noticeably upwards, passing back from a point vertically below the hind margin of the anterior hyomandibular facet (Fig. 2A). A similar inclination, but starting further forward, is seen in *L. mariae, L. microlepis* and *Luciolates stappersi* ; all other living species have this region of the skull in virtually the same line as the anterior part of the parasphenoid (cf. Fig. 1B with Fig. 2A).

Without an entire neurocranium it is impossible to form a precise opinion about the proportions of the otico-occipital region. Its narrowness has been noted already. If comparable-sized specimens of *L. calcarifer* and *L. niloticus* are compared with *L. rhachirhinchus*, then the otic region (exoccipital to the anterior prootic border) of the latter is relatively more elongate. As the only available skeletons of other *Lates* species and of *Luciolates stappersi* are much smaller than any fossil skull, a direct comparison is not feasible. However, the otic region in *L. rhachirhinchus* gives the impression of relative elongation, except possibly when compared with *Luciolates*. Another impression is that the cranial vault in *L. rhachirhinchus* is lower and flatter than in other species, and that this is attributable to a relative decrease in the depth of those bones lying above the level of the hyomandibular facets.

PARASPHENOID. Throughout its length, the ventral surface of the parasphenoid is rounded in the transverse plane, especially in the orbital region. Below the otic region the parasphenoid has a slightly flatter cross-section, and is marked by a deep and broad median groove which is almost continuous with a shorter and narrower groove in the basioccipital. The parasphenoid groove terminates anteriorly at a point immediately below the lateral commissure (Fig. 2).

The rounded cross-section and the median groove are characters not found in the parasphenoid of any extant *Lates* species.

ETHMO-VOMERINE REGION. The description of this region is based mainly on one specimen, the only one in the whole collection showing a relatively undamaged ethmoid complex (Fig. 5). The vomer, however, is represented by several almost intact bones (Figs 6, 7).

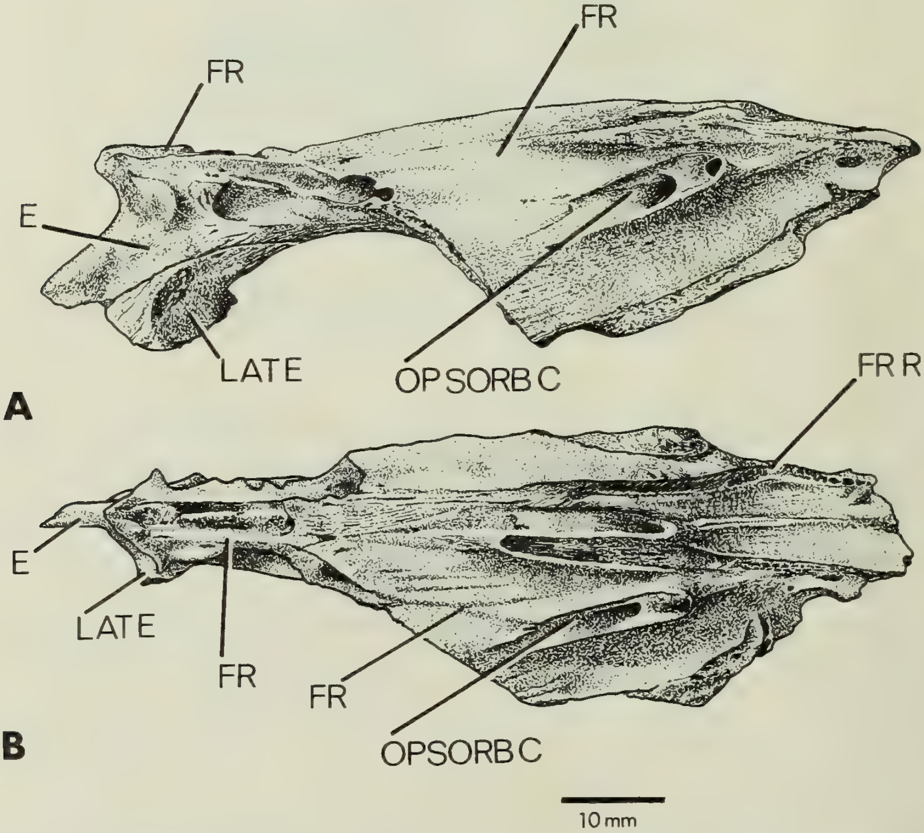

FIG. 5. *Lates rhachirhinchus.* Ethmoid and anterior frontal region of the skull. A. Slightly oblique dorso-lateral view of the left side. B. Dorsal view. (Paratype RG.17.525.)

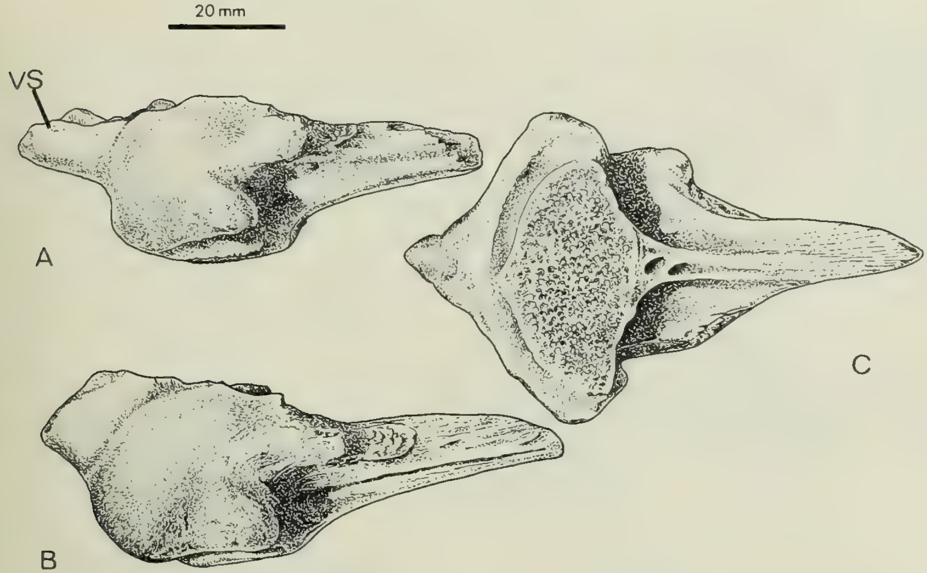

FIG. 6. *Lates rhachirhinchus.* Vomers. A and B. Left lateral views. C. Ventral view of B. A and B show variation in the angle of the vomerine spine ; in B this process is broken but in A it is almost complete. (Fig. 6A is the holotype ; other specimen from paratype lot RG.17.513–524.)

The vomer is a most characteristic element, quite unlike that found in any extant species, despite its basic similarity in shape. The median crest, instead of sloping gently upwards and backwards, is inclined forwards and resembles a laterally compressed horn (Fig. 7). There appears to be some intraspecific variability in the angle made by the horn to the body of the vomer. In some specimens the horn is almost horizontally aligned but in others it slopes upwards at an angle of *c* 45 degrees to the horizontal (Fig. 6). No specimen has the upper surface of the horn entire and thus it is difficult to determine how or where the ethmoid joins the process. In extant species the ethmoid suture is almost vertical, with the median crest of the ethmoid becoming continuous with the vomerine crest. The only fossil ethmoid available is damaged antero-ventrally, but judged on its general orientation it seems likely that the ethmo-vomerine suture was horizontally aligned. If this were so, then the ethmoid crest would join the vomerine horn to produce an ethmo-vomerine ridge projecting forward above and in advance of the body of the vomer.

A distinct furrow separates the vomerine crest from the body of the bone, the lateral margin of each furrow continuing forwards and downwards as a ridge over the anterior peak of the bone (Fig. 6A, B). Anteriorly, and between the ridges of each side, the vomer has a blunt, almost flat, entry angle.

The vomerine tooth patch is delimited by a distinct shelf from the edge of the vomer itself. This gives it the appearance of a plate fused with the vomer rather than, as in living species, of being an integral part of the bone (Fig. 6C). There is considerable individual variability in the shape of the vomerine tooth patch, even amongst specimens from one site ; apparently this variability is in no way correlated with size (see Fig. 7). The posterior margin of a tooth patch may be straight, slightly concave or produced into a low peak. The anterior outline varies from near-circular through cardiform to a laterally elongate near-rhomboid.

There is a well-defined facet for articulation with the palatine situated above and immediately behind each of the lateral projections from the vomerine body. The shaft of the vomer, in its shape and proportions, is like that in living species.

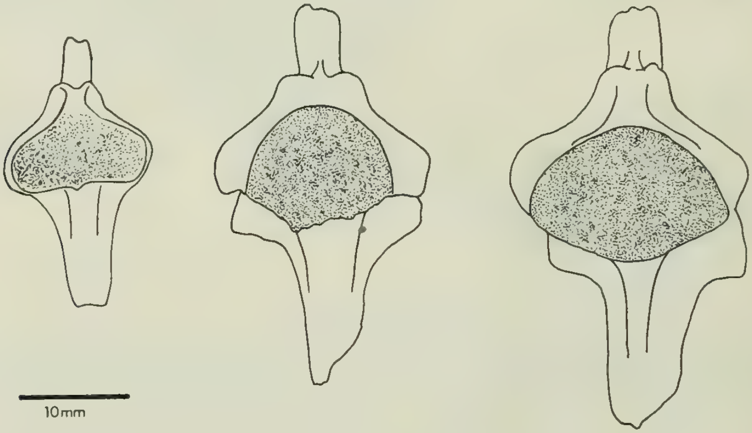

Fig. 7. *Lates rhachirhinchus*. Vomers, in ventral view, to show variation in the shape of the tooth patch.

Information on the ethmoid complex is derived exclusively from a single specimen (Fig. 5) comprising the greater part of the ethmoid, the left lateral ethmoid (virtually intact save for the lateral projection that articulates with the lachrymal bone) and the supraorbital and immediately postorbital parts of the left frontal. Except for a narrow strip along the midline, the right frontal is destroyed. We estimate that these bones are from a skull *c* 12 cm long.

The mesethmoid differs little from that in extant species, apart from its marked lateral compression, in which feature, as might be expected, it resembles *Luciolates stappersi*, another narrow-skulled form. Also, in *L. rhachirhinchus* the two dorsal projections underlying the dermethmoid are, as compared with all living forms, reduced to mere laterally directed and low ridges with no forward projection at all. In extant taxa the projections are horn-like and extend forward well beyond the outline of the median ethmoidal ridge.

The lateral ethmoid compares closely with that bone in *L. niloticus* except that it is much less extensive laterally and does not stand away from the skull as a distinct bony shelf. In this respect *L. rhachirhinchus* differs markedly from *Luciolates* and the endemic Lake Tanganyika species of *Lates*. In these the lateral ethmoid not only extends laterally but also downwards and backwards, giving the appearance in lateral view of a solid triangular wedge linking the vomer with the orbital margin.

No trace could be found of a foramen for the olfactory nerve, nor is there any indication that it might have been destroyed. Instead, in this region of the ethmoid there is a shallow, blind pit on the orbital side of the bone. Presumably the narrow ethmoid in *L. rhachirhinchus* obviates the need for a foramen, and the olfactory nerve therefore would pass directly from the orbit onto the lateral face of the ethmoid.

PALATOPTERYGOID ARCH. This complex is represented by two palatines only. In several details the autopalatine of *L. rhachirhinchus* differs from that of all extant *Lates* species. The most obvious difference lies in the shape and orientation of the maxillary process (Fig. 8) which, in the fossil, is more sharply angled relative to the dentigerous surface. As a result the process lies almost parallel to the dentigerous surface. Furthermore, the ridge from which the process arises is more prominent and, anteriorly, there is a distinct shoulder of bone extending medially and somewhat posteriorly from the base of the process. Compared with that in extant species, the dorsal facet of the maxillary process is poorly defined and lies further dorsally ; the ventral vomerine facet, although well-defined, is smaller and directed further ventrally in *L. rhachirhinchus* than in the extant species.

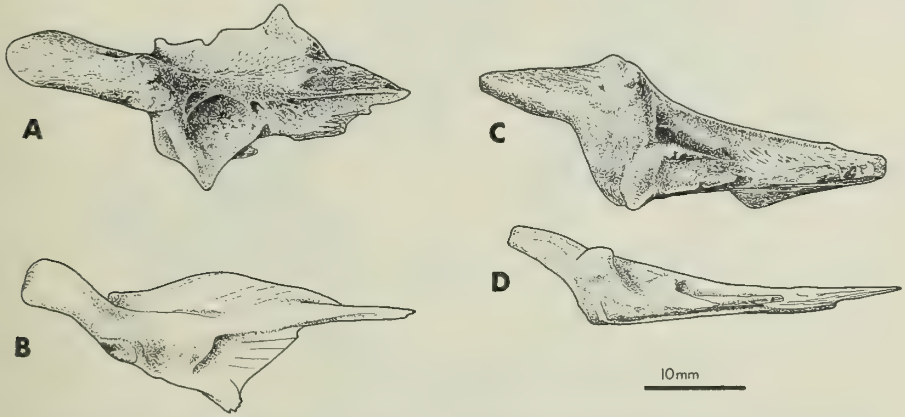

FIG. 8. Palatines (right) of : A and C. *L. rhachirhinchus* (paratype RG.17.593) ; B and D. *L. niloticus* for comparison. A, B dorsal views ; C, D medial views.

In all these features the autopalatine of *L. rhachirhinchus* closely resembles that bone in an unnamed *Lates* species from the Pliocene of Wadi Natrun (Greenwood 1972 : fig. 2).

UPPER AND LOWER JAWS. *Maxilla* (Figs 9, 10). No entire maxilla is preserved but there is a sufficiently large number of maxillary heads to show that this end of the bone differs in several respects from the maxilla in other species of *Lates* and in *Luciolates*.

In *L. rhachirhinchus* the dorsal process, for articulation with the ethmoid-vomer, is relatively higher and more rectangular in outline. The premaxillary process differs in having a less well-defined articulatory process on the portion directed ventro-medially, which in turn is separated from the dorsal portion by a deeper and more distinct groove (Fig. 9) running laterally at an angle of *c* 45 degrees. In extant species this groove is horizontal. Another difference in the premaxillary process is the way in which it is drawn out into a lip-like projection ; in extant species this region does not extend forwards beyond the dorsal part of the process, and the articulatory surface is larger and more clearly circumscribed (Fig. 9). A survey of the premaxillary process in extant *Lates* species (including *Luciolates stappersi*) also shows that this articulatory process is vertically or almost vertically inclined, whereas in *L. rhachirhinchus* it lies almost horizontally.

Behind the maxillary head, and immediately posterior to the saddle on which the palatine articulates, there is a very prominent spur of bone to which could have been attached the tendon for the *adductor mandibulae* I muscle. No extant species has such a well-developed process ; in these fishes it has the form of a low ridge (Fig. 10).

Premaxilla. In *L. rhachirhinchus* this bone is also distinctive. Again there are no complete specimens, but several fragments from the dentigerous area and anterior region are preserved. The description which follows is concerned only with the anterior region of the bone since it alone shows diagnostic features.

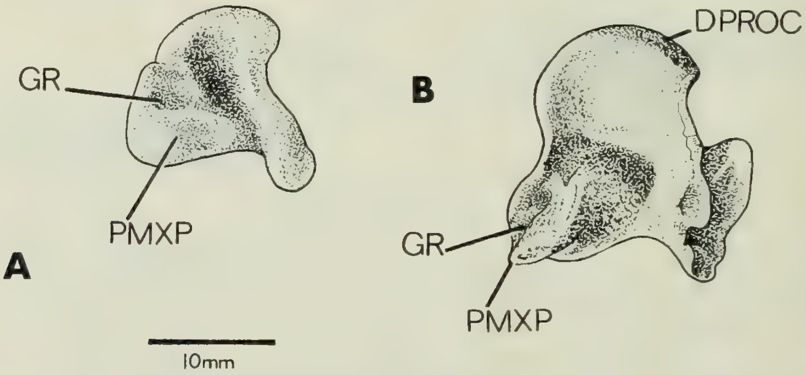

Fig. 9. Maxillae. Anterior view of the left maxillary head in : A. *L. niloticus*, and B. *L. rhachirhinchus* (from paratype lot RG.17.575–577).

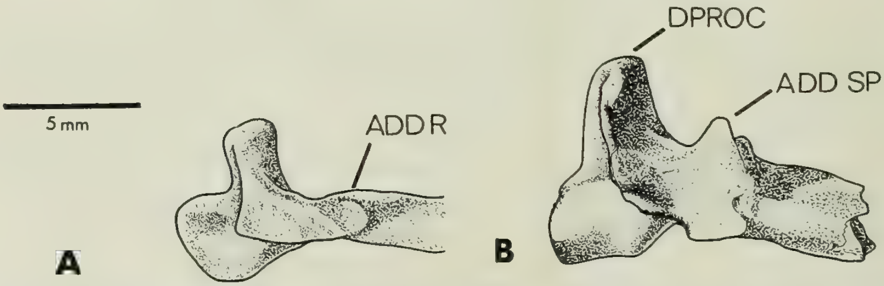

Fig. 10. Maxillae. Lateral aspect of left maxilla in : A. *L. niloticus*, and B. *L. rhachirhinchus*, to show the spur for attachment of the *adductor mandibulae* I muscle (from paratype lot RG.17.575).

When viewed laterally, the dentigerous surface, unlike that in extant species, is not continued forwards to form a narrow ledge skirting the anterior face of the bone (Figs 11, 12). Instead, it fails to project beyond the anterior margin. The articular process in *L. rhachirhinchus* is larger, especially broader, than in extant species. When seen from above, it lies at an angle to the ascending process (not in the same line) and is inclined medially (not vertically as in the living species). Extant *Lates* and *Luciolates* have a discrete median arm extending inwards from the lateral, shield-like portion of the articular process. In *L. rhachirhinchus* this arm is barely represented by a low basal ridge (Fig. 12).

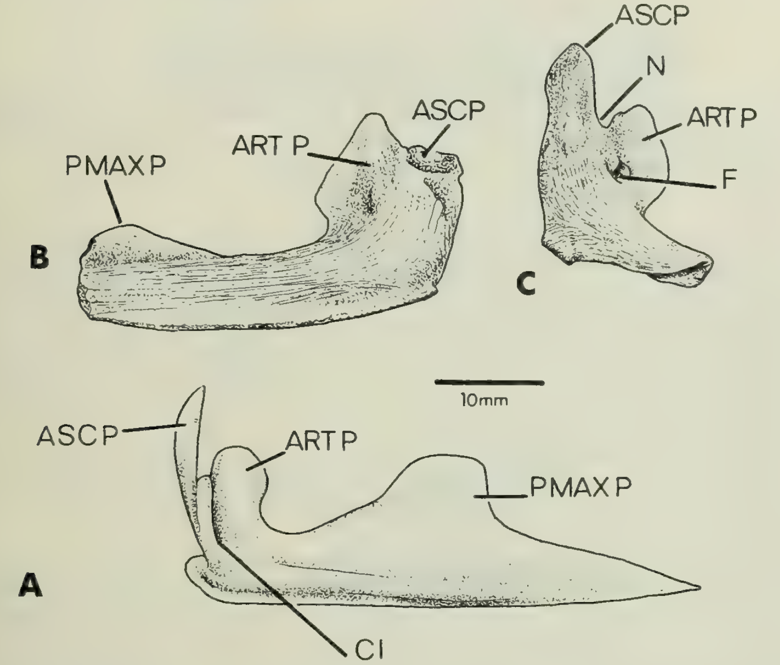

FIG. 11. Premaxillae of: A. *L. niloticus* in left lateral view; B. *L. rhachirhinchus* in right lateral view; C. *L. rhachirhinchus*, anterior part of premaxilla showing ascending and articular processes, and the foramen in the latter. (Specimens figured in B and C are from paratype lot RG.17.572.)

The stout ascending process is inclined somewhat forwards in *L. rhachirhinchus*, but in other species it is bowed and curves gently backwards. In all extant species, including *Luciolates stappersi*, the process is more slender and is separated from the articular process by a deep but narrow cleft extending almost to the bases of the two processes. *Lates rhachirhinchus*, in contrast, has the articular process fused to the ascending process over the greater part of its length; a shallow notch, slightly below the tip of the articular process, is all that remains of the cleft (Fig. 11). A unique feature of the premaxilla in *L. rhachirhinchus* is a large foramen that opens

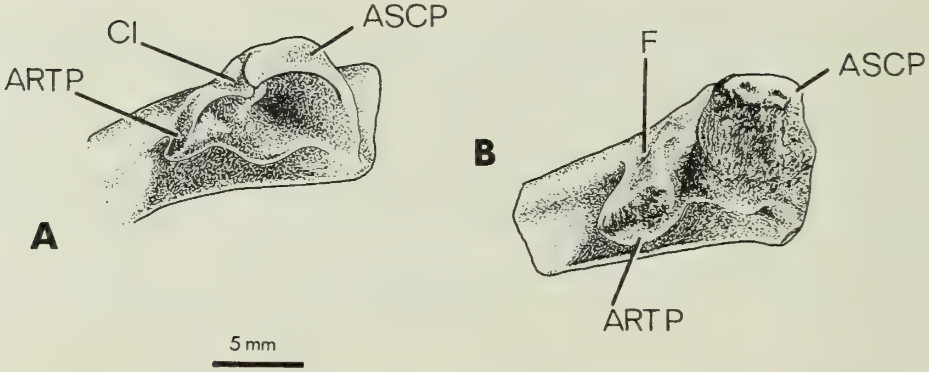

FIG. 12. Premaxillae of: A. *L. niloticus*, and B. *L. rhachirhinchus* (from paratype lot RG.17.572). In both, the anterior end of the bone is seen from above to show the relationship of the articular and ascending processes.

medially below the notch, then passes obliquely downwards and opens laterally near the base of the articular process. No trace of this foramen is found in any living species ; presumably in *L. rhachirhinchus* it provided a passage for a branch of the maxillary nerve and perhaps also for a blood vessel. In *Lates niloticus* a large blood vessel passes through the cleft between the ascending and articular processes, and several nerves pass outwards and downwards on the lateral face of the premaxilla.

No specimen of a *L. rhachirhinchus* premaxilla is sufficiently complete for us to determine accurately the size of the posterior maxillary process ; where some of the process is preserved it seems to be lower than in other species.

No bone can be identified as a supramaxilla.

Dentary. Unlike the jaw bones described so far, the dentary in *L. rhachirhinchus* seems to depart but slightly from that bone in extant species. The only differences we could detect are the relatively longer openings to the lateral-line sensory canal and a relatively narrower dentigerous surface (Fig. 13). It must, however, be remembered that only the anterior portion of the dentary is preserved in our specimens.

As with the premaxilla, the pattern of densely packed and small bones of attachment on the dentary suggests that the teeth and dental pattern were similar to those in living *Lates* species. Certainly there are no indications of an outer row of enlarged teeth like those on the dentary of *Luciolates stappersi*, nor of the few enlarged anterior premaxillary teeth such as occur in the premaxilla of that species.

Angulo-articular. Most specimens are incomplete, and comprise only that area of the bone around and forming the articulatory facet for the quadrate head. Compared with the angulo-articular in other *Lates* species, that of *L. rhachirhinchus* has a deeper facet, distinctly bowl-shaped in lateral outline, with the posterior face rising more steeply, almost at a right angle, and its tip curving anteriorly (Fig. 14).

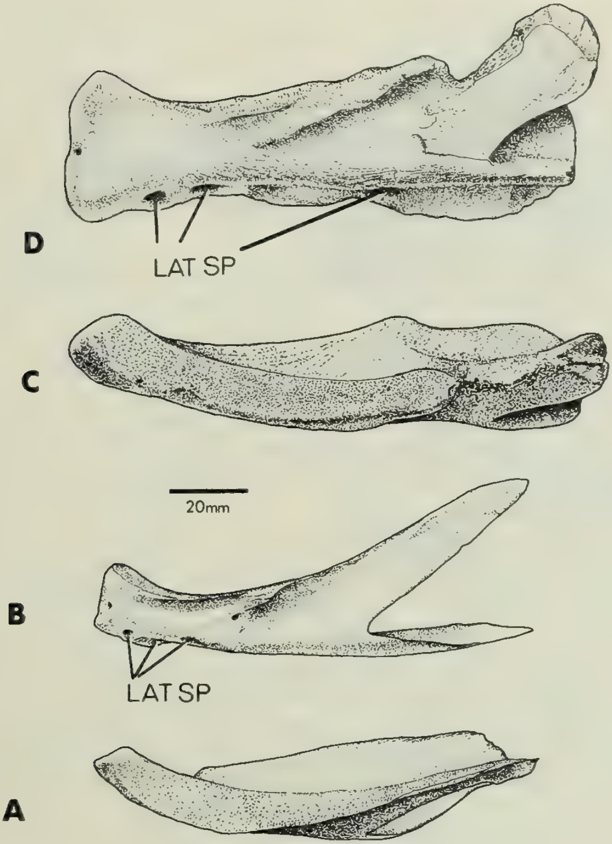

FIG. 13. Dentaries of : A and B. *L. niloticus*, occlusal and left lateral views respectively ; C and D. *L. rhachirhinchus*, occlusal and left lateral views (paratype RG.17.540).

Also, the groove for the latero-sensory canal which underlies the facet is deeper and longer in this species.

Retroarticular. This is present in two specimens ; it is a stout and relatively triangular bone, differing in these respects from the larger and less regularly shaped retroarticular in all extant species except *L. calcarifer*. In that species the bone does resemble the retroarticular of *L. rhachirhinchus*.

Quadrate. In *L. rhachirhinchus* (Fig. 15) this is very similar to the quadrate in all other *Lates* species, except that the articulatory head and the adjacent antero-ventral limb of the bone slope ventromedially at an appreciable angle, being horizontal in other species.

SUSPENSORIUM, OPERCULAR AND BRANCHIAL SKELETONS. Apart from several gill rakers and one bone tentatively identified as an epihyal, no recognizable elements of these skeletal systems are represented in the collections. The gill rakers are of

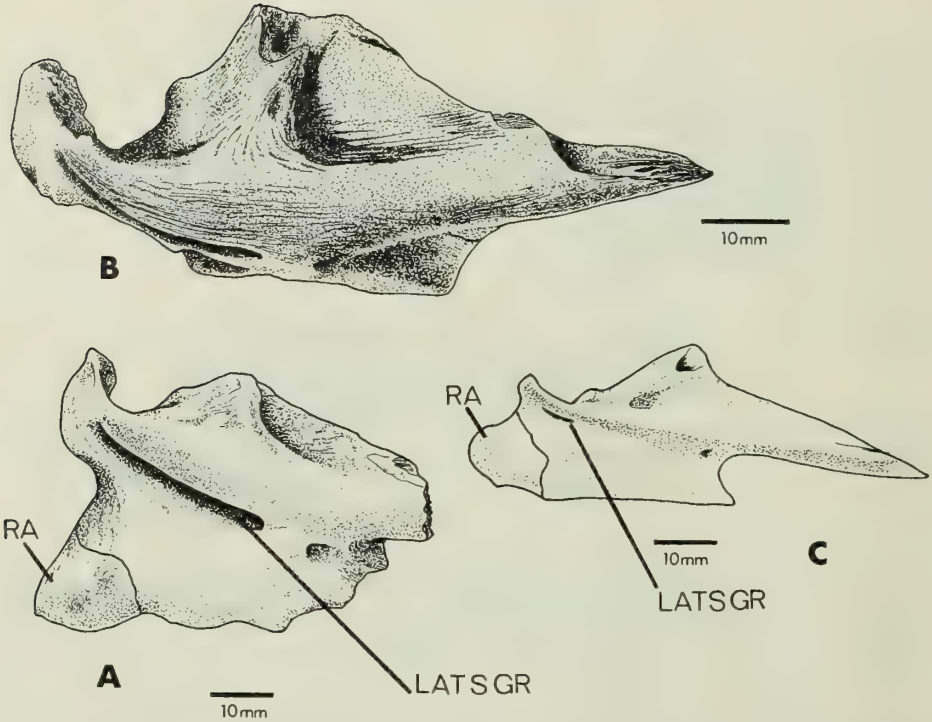

FIG. 14. Angulo-articulars, right bone in lateral view, of: A and B. *L. rhachirhinchus*; C. *L. niloticus*. The retroarticular is present in A and C. (Specimens shown in A and B are paratypes RG.17.591 and 17.590 respectively.)

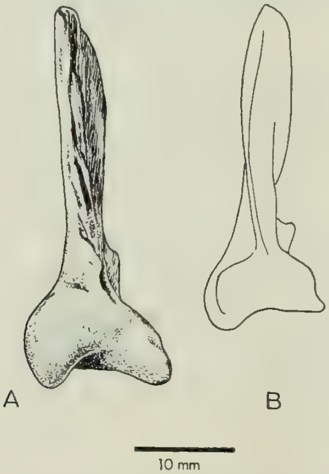

FIG. 15. Quadrates. Anterior aspect of right quadrate in: A. *L. rhachirhinchus* (paratype RG.17.570), and B. *L. niloticus* (outline only), to show differences in the shape of the articular surface.

the elongate type which forms the outer row of rakers on the first gill arch in extant species. The fossil rakers closely resemble those in *L. niloticus*, but appear to be relatively wider at the base.

The presumed epihyal is a fragment that may be the posterior half of that bone. It differs quite markedly from the epihyal of extant *Lates* in several features, including its thickness, the concavity in its posterior ventral outline (straight or convex in other species) and in details of the presumed articular surface for the interhyal.

Reference can be made here to several fragments of bone which, from their general morphology, may be branchiostegal rays. Since these bones are mere fragments, and because they differ in several small details from the branchiostegal rays of living *Lates* species, our identification must be considered as very tentative.

VERTEBRAL COLUMN. Almost without exception, the vertebrae in this collection consist of damaged centra. The few exceptional specimens have the neural or haemal arch, or both, still attached but in none is the entire neural or haemal spine preserved.

Apart from the first and third abdominal vertebrae, it is difficult to establish the exact position of a centrum in the column. This difficulty is due in part to the results of damage and in part to morphological differences existing between the fossil centra and those of extant species. We have, therefore, attempted to identify and describe only the first six abdominal centra. The presumed position of these elements has been arrived at on the basis of overall similarity between a fossil specimen and a particular vertebra in the extant species. When dealing with centra posterior to the third we have placed special emphasis on the socket in which the pleural rib articulates.

The peculiar overall morphology of the first and third centra is shared by fossil and living species, thus making the identification of these elements quite definite. No centrum is identified as being from the second abdominal vertebra of *L. rhachirhinchus*. One centropomid second vertebra is, however, recorded from Sinda-Mohari Point 6. The deposits here are considerably younger than those yielding the type specimens of *L. rhachirhinchus*, and it is interesting to note that most of the *Lates* remains from Point 6 are attributable to a species close to, if not identical with, *Lates niloticus* (see p. 115). The second vertebra, too, is indistinguishable from that of *L. niloticus*.

First vertebra (Fig. 16). There is some intraspecific variability in the shape of the centrum. Many specimens have the centrum clearly shorter ventrally than dorsally, i.e. when it is viewed laterally it tapers gradually from top to bottom. The width of the anterior face is but slightly greater than its depth, and the trabeculae running from the exoccipital facets are tightly arranged and extend obliquely across the entire length of the centrum.

Variants of this common type include centra of almost uniform length dorsally and ventrally, others with loosely arranged trabeculae immediately below the facet which merge imperceptibly with those on the body of the centrum, and, less

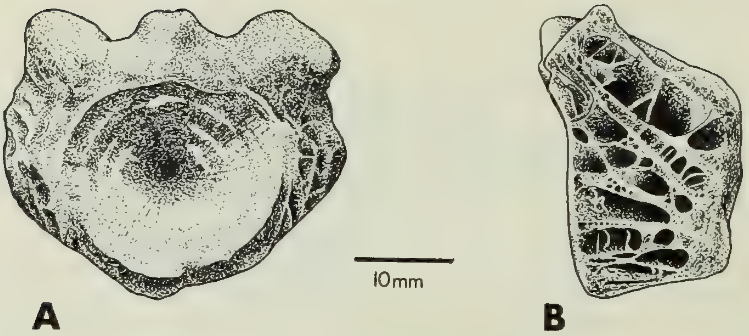

FIG. 16. *Lates rhachirhinchus.* First abdominal vertebra in : A. anterior, and B. left lateral views. (Paratype RG.17.594.)

frequently, some centra that are noticeably wider than deep (i.e. about 1½ times, as compared with 1 to 1⅓ times in the others).

Whatever the characters of the central body, its exoccipital facets have a constant and characteristic form. They are confluent medially, with the zone of contact thrown upwards into a saddle-shaped area projecting well above the plane of the facets. Only in *L. calcarifer* and *L. microlepis* amongst extant species does one find a condition approaching that in *L. rhachirhinchus*. The first vertebra of *L. rhachirhinchus*, however, differs from that in all other *Lates* species in having a relativlye smaller facet area. As a result of this reduction in size, a vertical dropped from the posterior rim of the facet falls just behind the anterior face of the centrum and not,

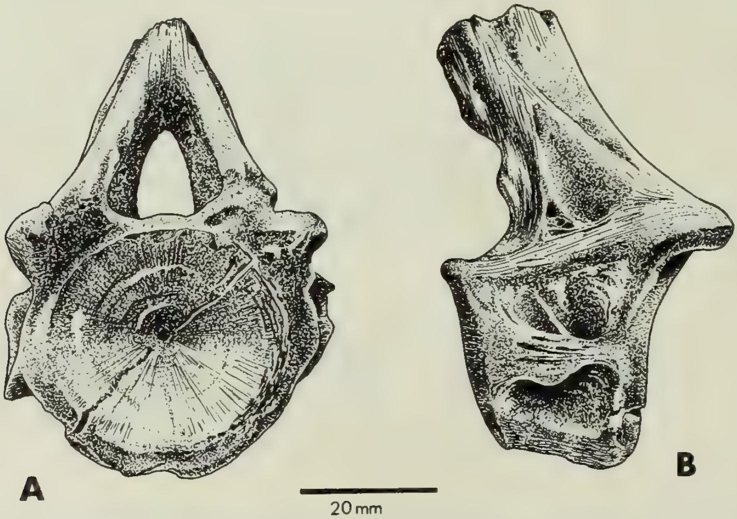

FIG. 17. *Lates rhachirhinchus.* Third abdominal vertebra in : A. anterior, and B. right lateral views. (Paratype RG.17.595.)

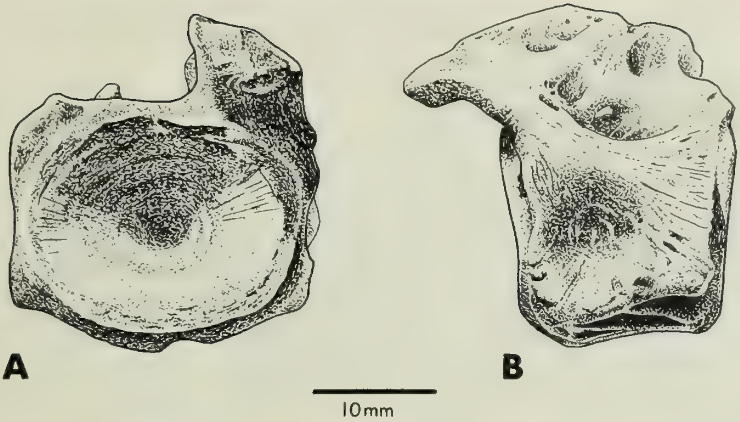

FIG. 18. *Lates rhachirhinchus.* Fourth or fifth abdominal vertebra in : A. anterior, and B. left lateral views. (Paratype RG.17.596.)

as in other species, to a point near the middle of the centrum or even a little further posteriorly. The angle of inclination on the facets is similar in all species, including *Luciolates*.

Third vertebra (Fig. 17). The proportions of this centrum, which is somewhat compressed antero-posteriorly, are like those in extant species. However, the anterior face is more concave and lacks the narrow but prominent collar of bone lying concentrically and immediately within the bevelled outer margin. The posterior face has about the same degree of concavity in *L. rhachirhinchus* and the living species, although in the former the margin is more distinctly bevelled, and there is a broad, concentric ridge surrounding the concavity. In other words, the situation on the posterior face in *L. rhachirhinchus* vertebrae is like that on the anterior face in extant species.

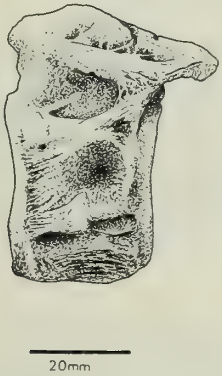

FIG. 19. *Lates rhachirhinchus.* Fourth or fifth abdominal vertebra in right lateral view, to show variability in this centrum. A non-typical specimen ; compare Fig. 18.

The prezygapophyses are well-developed, and the deep glenoid facet for the pleural rib lies immediately below the bony brace extending between the pre- and postzygapophyses.

Fourth or fifth vertebrae (Figs 18 and 19). No more precise location can be determined for centra assigned to this position in the column. This uncertainty is because the fossil centra do not resemble at all closely their presumed counterparts in extant species. The centra are assigned to a 'fourth–fifth' position because they have the rib facet situated ventro-laterally, and because there is no trace of an incipient 'transverse process' such as occurs on the sixth and seventh vertebrae in extant species.

In extant species the rib facet on the fourth vertebra lies high on the centrum, occupying about the anterior half of its dorsal moiety. The fifth vertebra in these species has the facet placed much lower down, almost entering the ventral outline of the centrum.

The facet occupies a ventro-lateral position in all the *L. rhachirhinchus* centra assigned to a 'fourth–fifth' position. Its lower margin is produced to form a distinct gutter-like lip, a feature not observed in any extant species. Amongst our specimens there is some variation in the extent to which the lip is developed, and a correlated variation in the position of the facet. Those centra with the more ventral facet are presumed to be the fifth vertebra.

If our specimens represent a mixture of both fourth and fifth centra then the situation in *L. rhachirhinchus* is quite unlike that in any other species of the genus, not only in the details noted above but also in having the two vertebrae so similar. But the likelihood of these centra being mostly or even entirely from fourth vertebrae is indicated by a specimen of two centra still in articulation. One member of this pair is of the type we identify as a third vertebra ; the other closely resembles the majority of centra classified in the category 'fourth or fifth'. Thus, either the fifth vertebra is represented by those centra which differ slightly from the modal type, or else the centra we have tentatively identified as the 'sixth and seventh' are in fact the fifth and sixth vertebrae respectively.

Be that as it may, there are indications that the centrum of the 'fourth or fifth' vertebra shows size-correlated changes in proportions. The three smallest specimens (breadth of anterior face 11·0, 12·0 and 14·0 mm ; length of centrum 10·0, 10·0 and 12·0 mm respectively) have proportions like those of similar-sized fifth centra in *L. niloticus*. Larger centra, however, are relatively broader (i.e. breadth 23·0, 30·0, 33·0 and 36·0 mm ; length 14·0, 22·0, 18·0 and 22·0 mm for the centra respectively), and differ similarly from centra in *L. niloticus* of comparable size. Full comparison with other *Lates* species and with *Luciolates* is precluded by the absence of large specimens of these species.

? *Sixth vertebra*. The one relatively undamaged specimen on which this description is based has small 'transverse processes', first seen on the sixth vertebra of *L. niloticus* and all other species, hence our identification of the fossil as being that vertebra. The rib facet is small and lies above and behind the transverse process.

? *Seventh vertebra* (Fig. 20A). The 'transverse process' on this centrum is but slightly better developed, although the rib facet has virtually disappeared.

Other abdominal and caudal vertebrae. Since it is impossible to determine column position for these centra, they cannot be compared directly with their counterparts in extant *Lates* and *Luciolates* species.

Two morphotypes are represented in the collection. One (Fig. 21) has the appearance and proportions of posterior abdominal and caudal vertebrae in *L. niloticus*, *L. calcarifer*, *L. macrophthalmus*, *L. angustifrons* and *L. microlepis*, and of the posterior abdominal and anterior caudal vertebrae only in *L. mariae*. *Luciolates stappersi* is not mentioned here because all its posterior abdominal and caudal centra have a characteristically elongate form as, indeed, do the anterior abdominal centra as well.

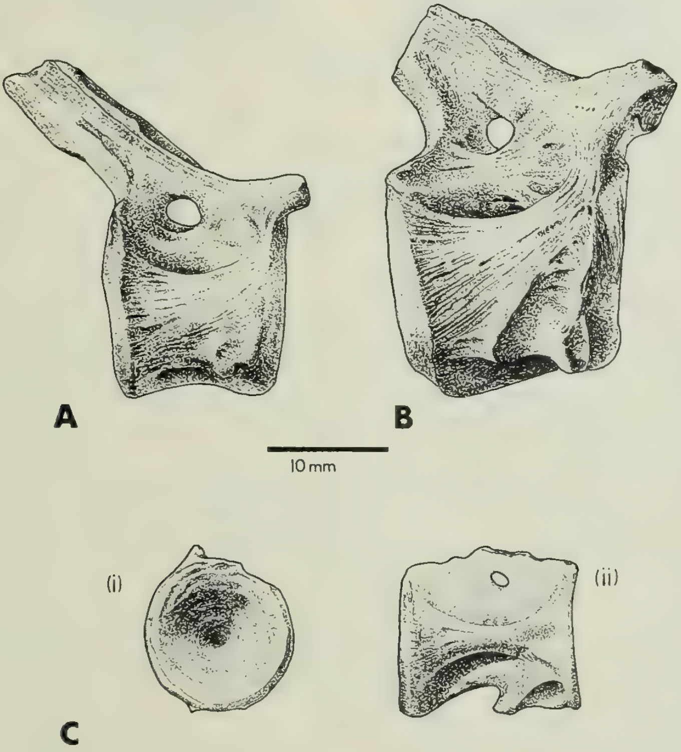

Fig. 20. *Lates rhachirhinchus*. A. ? Seventh abdominal vertebra in right lateral view, non-typical specimen. B. ? Eighth abdominal vertebra, in right lateral view, non-typical specimen. C. Posterior caudal vertebra (elongate type) in (i) anterior and (ii) right lateral views, non-typical specimen.

The second type of fossil centrum (Fig. 20C) is more elongate, with a distinctly compressed middle section that gives it a waisted, almost hourglass-shaped outline. They closely resemble the posterior caudal centra of *L. mariae* and all caudal centra in *Luciolates stappersi*.

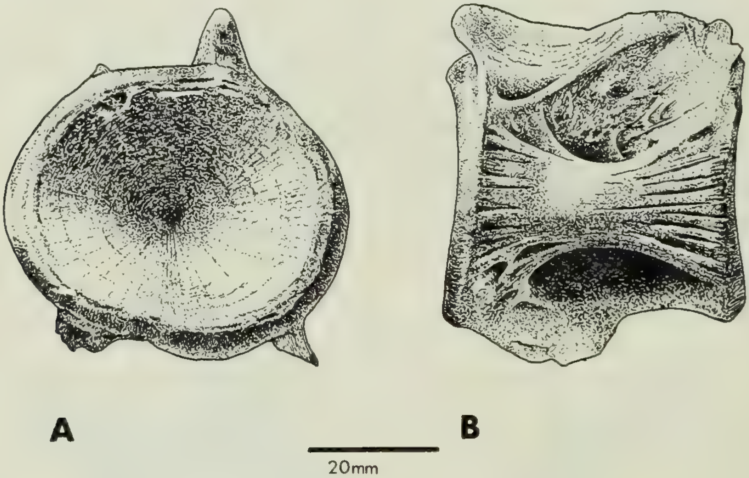

FIG. 21. *Lates rhachirhinchus*. Posterior abdominal vertebra in: A. anterior, and B. left lateral views. (Paratype RG.17.597.)

From this we conclude that there is in *L. rhachirhinchus* a gradient of centrum shape and proportions like that in *L. mariae* amongst extant forms. It may be noted in this connection that, relative to species in the *L. niloticus* complex, *L. microlepis* of Lake Tanganyika has somewhat more elongate caudal centra, particularly in the middle section of that region in the column. This differentiation, like that found in the other Lake Tanganyika species *L. mariae* and *Luciolates stappersi*, may be correlated with the more elongate and slender body form of these taxa, even as compared with the one other endemic species from that lake. To judge from the skull proportions of *L. rhachirhinchus*, this species had a body form more like that of *L. microlepis* or *L. mariae* than that of *L. niloticus* or its close relatives.

Urostylar vertebrae. The few (4) specimens of fused first ural and first preural centra available show no outstanding characters ; in two the fourth hypural is still attached.

OTHER SKELETAL REMAINS including fin rays and supporting bones. Little of the pectoral girdle and its associated bones is preserved. There is part of a scapula (the articular surface) and a fragment of bone thought to be part of an extrascapula. Neither bone shows any specifically diagnostic features.

Nothing can be identified as coming from the pelvic girdle, except for the proximal end of a large pelvic spine. However, since this specimen is from Sinda-Mohari

Point 6 (see p. 115) it is not necessarily from *L. rhachirhinchus*. Certainly it provides no features to distinguish it from a spine of *L. niloticus*.

The collection does contain a large number of percoid dorsal and anal fin spines, some complete but the majority damaged. Since most of the specimens are from Sinda-Mohari Point 10 it is very probable that they were derived from *L. rhachirhinchus*, although the possibility of at least the smaller specimens coming from a large cichlid fish (e.g. *Sarotherodon*) cannot be set aside.

Relationships of *Lates rhachirhinchus*. As yet there is no published account of any detailed arguments supporting a postulated phyletic arrangement of species within the genus *Lates*, nor of the relationships between these taxa and *Luciolates stappersi*. Sorbini (1973) reviewed the relationship between *Lates* and the Eocene taxon *Eolates*, and also considered the status of certain extinct *Lates* species. But, because Sorbini has made only a moderately detailed study of one extant *Lates* species and did not consider *Luciolates*, his conclusions must be viewed with certain reservations.

One of us (P. H. G.) is currently investigating the interrelationships of *Lates* species and their relationship with *Luciolates* ; our assessment of the phylogenetic position of *L. rhachirhinchus* is to a large extent based on provisional conclusions stemming from that study.

There appear to be two major lineages within *Lates*. One line comprises the endemic species of Lake Tanganyika (*L. angustifrons*, *L. mariae*, *L. microlepis* and *Luciolates stappersi*). The other line comprises *L. calcarifer*, *L. niloticus*, *L. macrophthalmus* and the extinct species *L. fajumensis* from Egypt. (For details of *L. fajumensis* see Weiler 1929.) The Tanganyikan lineage, including *Luciolates* whose generic status is under review, must be considered the derived (apomorph) sister group of the *L. calcarifer–niloticus* assemblage.

Lates rhachirhinchus has many derived characters that are not present in either of the lineages noted above – for example the vomerine spine, the poorly developed post-temporal fossa, and the various unique features in its jaw and associated bones. Indeed, we can find no derived features that are shared with the *L. calcarifer–niloticus* line. However, *L. rhachirhinchus* does share at least one apomorph feature with all members of the Tanganyika lineage, namely narrowing of the skull, and another, marked morphological differentiation between anterior and posterior caudal centra (p. 96), with two members of that line. All members of the Tanganyika lineage, including those species without a clear-cut differentiation in centrum shape, show apomorph features not found in *L. rhachirhinchus* and thus are more closely related *inter se* than is any one species with *L. rhachirhinchus*. Nevertheless, the affinities of the latter species seem, on the basis of skull form and vertebral characteristics, to be with the Tanganyika species rather than with *L. niloticus* and its immediate relatives.

It still remains to ask whether these resemblances are manifestations of convergence rather than an expression of close phyletic affinity, a question rendered more pertinent by the suite of unique apomorph characters found in *L. rhachirhinchus*. For example, does *L. rhachirhinchus* represent a taxon derived from a *L. niloticus*-like ancestor which evolved rapidly in a local and isolated water body while its sister species continued to exist, unchanged morphologically, in neighbouring waters? The evolution during the Pleistocene of a distinct species (*L. macrophthalmus*) in Lake Albert, and of a so-called subspecies (*L. niloticus longispinis*) in Lake Rudolf, shows that isolated populations of *L. niloticus*-like species do respond to this type of evolutionary situation, albeit in these examples with less morphological divergence than is seen in *L. rhachirhinchus*. If such should have been the evolutionary history of *L. rhachirhinchus*, then the apomorph characters shared with the Tanganyika lineage would be of no value as indicators of its true phylogeny.

On the other hand, the specializations it has in common with the Tanganyika lineage could reflect a relationship with the ancestral species of that flock, assuming that the lineage had branched off from the *L. niloticus* group before it entered the Lake Tanganyika basin.

For the moment there is no evidence which will enable us to test either hypothesis, and so phyletically *L. rhachirhinchus* must be kept *incertae sedis*. One conclusion is, however, definite. During the early Quaternary there existed in eastern Africa a *Lates* species showing far greater morphological differentiation than either *L. calcarifer* or *L. niloticus*, the two most generalized extant members of the genus.

The temporal and geographical distribution of *L. rhachirhinchus* may well have been restricted. A species of *Lates* is abundantly represented in deposits of Lower Pleistocene age at Kaiso, Uganda (White 1926), some 100 km to the north-east of Sinda-Mohari, and in Lower to Upper Pleistocene deposits at and near Ishango, some 150 km to the south-west (Greenwood 1959). The taxon represented by these bones is certainly not *L. rhachirhinchus*, nor are there indications of its being closely related to that species. Indeed, as far as can be told from the bones preserved, these Kaiso and Ishango fishes are indistinguishable from *L. niloticus*.

Possibly the latest record is from Lower Pleistocene (Villafranchian) beds at Sinda-Mohari, Point 6 (p. 115). Geographically, the centre of *L. rhachirhinchus* distribution is in the Sinda-Mohari area, with only one possible record from Nyamavi (p. 116) outside it.

Superorder OSTARIOPHYSI

Order CYPRINIFORMES

Family ? **CHARACIDAE**

The most outstanding fish remains in the entire collection are fifty-seven large and peculiarly shaped teeth derived from an undescribed characoid fish. Most of this material comes from outcrops on the left bank of the Sinda river, but a few specimens are from other sites in the Sinda-Mohari area, and one is from the Karugamania beds of Lake Albert (map, Gautier 1970 : fig. 1).

That these teeth are from a characoid fish is clearly demonstrated by comparative morphological and histological studies. Great difficulty was encountered, however, when we attempted to determine the family in which the fish should be placed. None of the teeth corresponds exactly with teeth from any extant African characoid (i.e. members of the families Characidae, Hepsetidae, Distichodontidae, Citharinidae or Ichthyboridae). A closer correspondence exists between some of these teeth and those found in certain neotropical Characidae of the subfamily Serrasalminae. The teeth that do not resemble Serrasalmine types have a peculiar cusp pattern otherwise known only from an extinct taxon currently referred to the genus *Alestes* (Greenwood 1972).

It is for these reasons that we are uncertain about the familial status of the taxon which these teeth represent. We have therefore placed it tentatively in the Characidae. A more definite conclusion might have been reached had there been any bones associated with the teeth. No characoid skeletal remains whatsoever are recorded from any of the sites we have studied. This absence is surprising and quite inexplicable. Most other fish taxa from these deposits are well represented by a variety of bones, and it is difficult to believe that the jaws associated with the characoid teeth were in any way more delicate or less likely to be fossilized than were these other bones.

Genus ***SINDACHARAX*** nov.

1972 *Alestes* (part) : Greenwood, 506–511 (*A. deserti*, see p. 104 below).

Diagnosis : Characoid fishes with a markedly heterodont dentition, in which some teeth are basically unicuspid (Fig. 23A), some very weakly tricuspid (Fig. 21A), and some are multicuspid with one major cusp and two or three serially arranged ridges of cuspules (Fig. 22B), a crown pattern not found in any extant characoid taxon (see below, p. 105).

Type species : *S. lepersonnei* sp. nov.

Sindacharax lepersonnei sp. nov.

Diagnosis : Differs from the only other known species in the genus (see p. 105) in the shape and proportions of its teeth, and in having the majority of cusp ridges on the premaxillary inner teeth composed of interconnected cuspules and not continuous ridges (cf. Figs 22–24 with Greenwood 1972 : pl. 1, figs 2–8).

Etymology. The species is named in honour of Dr Jacques Lepersonne of the Musée Royal de l'Afrique Centrale, Tervuren, as an appreciation of his contributions to African palaeontology and geology.

Holotype : A presumed premaxillary inner tooth (type 1) from sites nos 145 and 156 (surface finds derived from basal Sinda Beds) on the left bank of the Sinda river, Zaire (Fig. 22B, specimen c). RG.17.599.

Paratypes : Thirty-five other teeth from the same locality. RG.17.600.

Age and locality. The majority of teeth are from the Sinda-Mohari area (Gautier 1970 : fig. 1), and from the basal Sinda beds of presumed earlier Pleistocene (Lower Villafranchian) or uppermost Pliocene age (see p. 74 for further discussion on this dating). Three teeth are, however, from Miocene beds on the right bank of the Mohari river (outcrop L98), and another is from the Lower Miocene beds of Karugamania (*c* 12 km west of Lake Albert and some 20 km north of the Semliki delta region ; Gautier 1970 : fig. 1).

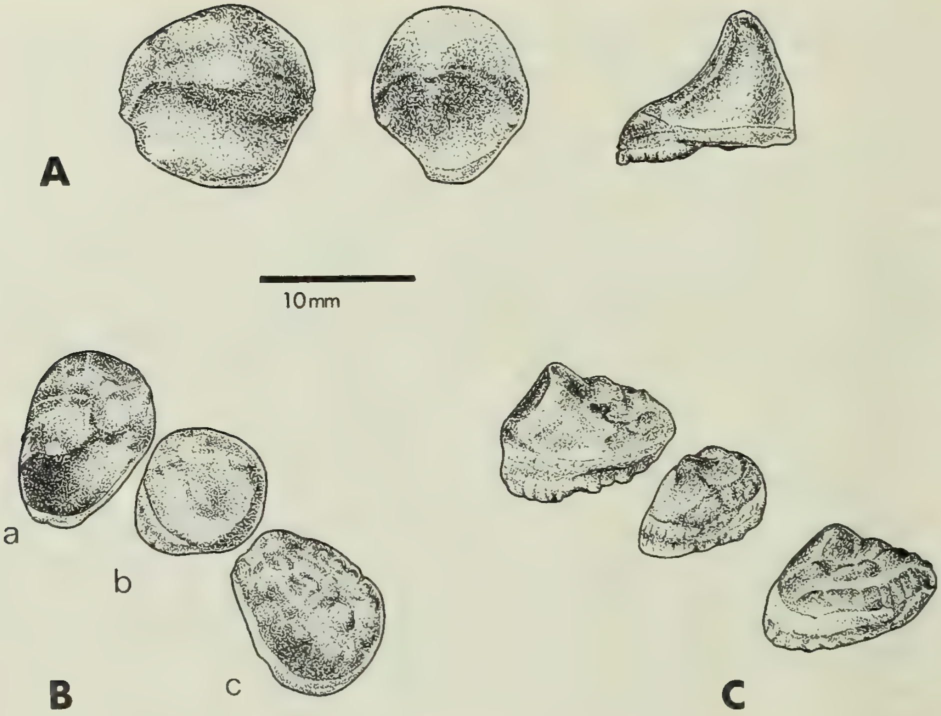

Fig. 22. *Sindacharax lepersonnei.* Premaxillary teeth. A. Outer row teeth ; from left to right : two teeth in occlusal view, one in lateral view (paratypes). B. Inner row teeth in occlusal view, and arranged as teeth from the left premaxilla (i.e. medial tooth on left of row, and labial face of teeth towards top of page). From left to right the teeth are : (a) Type II, (b) Type III, and (c) Type I. C. The same teeth but viewed from an anterior and lower position so as to give an oblique quartering view of their crowns. The lingual aspect of the teeth is towards the bottom left-hand corner of the page. (Paratype lots RG.17.599 and 17.600.)

Description. This is based on the 36 type specimens, although details were checked against the 21 specimens of the hypodigm (see pp. 107–115).

Without corresponding jaw bones it has proved difficult to establish from which jaw the various teeth were derived, and virtually impossible to tell precisely the position of a particular tooth in the tooth row of its jaw. Our identification of the jaw, and a tooth's position in that jaw, is based on the approximation of fossil tooth morphology to that of teeth in living *Colossoma* and *Alestes* species. It must be considered conjectural.

Upper jaw. Outer row (11 specimens). Only one form of tooth is represented in the paratypical sample, or amongst non-typical material. At first sight the tooth appears to be unicuspid and the cusp triangular, with its lingual face slightly concave and sloping steeply to the base where it becomes a narrow, near horizontal shelf

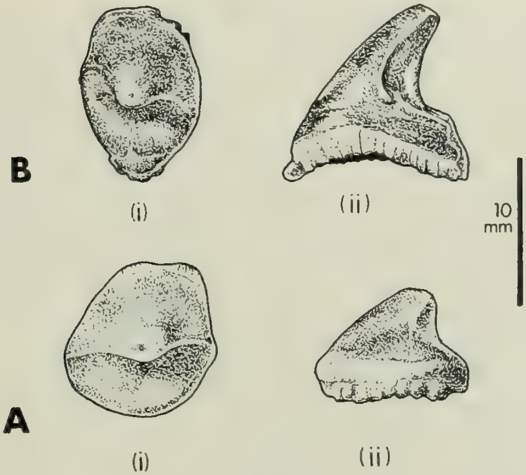

FIG. 23. *Sindacharax lepersonnei.* Dentary teeth. A. Tooth from outer row, in (i) occlusal and (ii) lateral views. B. Inner tooth in (i) occlusal and (ii) lateral views. (Paratype lot RG.17.600.)

(Fig. 22A). The cutting edge of the cusp, formed where the convex labial and concave lingual faces meet, has a clearly defined, broadly U-shaped outline, with the base of the U directed labially. On each side, at its junction with the base, there is a small, low cuspule. Thus, the tooth can be considered as a tricuspid in which the median cusp is disproportionately enlarged.

The base of the tooth is almost circular, with the bone of attachment plicate and deeply indented on each side at the point where the cutting edge meets the basal shelf. The longest horizontal axis of the occlusal surface measures, in the 11 specimens, 8·0 (frequency 3), 9·0, 10·0, 11·0 (f2), 11·5, 12·0 and 13·0 (f2) mm.

In their overall morphology these teeth closely resemble those in the anterior half of the outer premaxillary row of *Colossoma* species ; there is little similarity with outer premaxillary teeth in any *Alestes* species.

Inner teeth. Three different types of teeth are thought to be from the inner row of the premaxilla. In type 1 the occlusal outline is a distorted ovoid. On one margin there is an epicentrically placed cusp flanked on one side by a single low cusp and by three low cusps on the other (Fig. 22B, C) ; the entire row of five cusps is slightly curved. There is a second row of two, or more often three, cusps, also low and arranged in a gently curving arc that is a mirror image of the first row, which it meets. At least one cusp in this second row is noticeably elongate. The third row of cusps is more in the nature of an indented ridge than a series of discrete cuspules, although at the narrow end of the ovoid the cuspules are more distinctly separated. The curvature of this row parallels that of the second row. There are four teeth of this type, two from one side of the jaw and two from the other. The longest horizontal axis of each tooth measures 12·0, 13·0, *c* 14·0 and 15·0 mm respectively.

In type II teeth the occlusal outline is a distorted ovoid, the narrow end of which is thrown into a single high and conical cusp. One face of this cusp (the longest one) slopes more steeply than the others so that, in effect, its apex is situated somewhat eccentrically. A ridge of three low, blunt cusps, one more elongate and discrete than the others, is arranged in a gentle curve, the concave side of which faces the single major cusp (Fig. 22B, a). Beyond this cusp ridge, and at a lower level, is a curvilinear ridge of about five or six poorly demarcated cusps. It parallels the first ridge and forms the occlusal margin of the crown. There is one well-preserved tooth of this type, and one badly worn specimen. The longest horizontal axis of each tooth measures 12·0 and *c* 8·0 mm respectively.

Type III teeth have an almost circular occlusal outline. The crown is dominated by a distinct central cusp whose wide but compressed shoulders form a crest extending across almost the complete diameter of the crown. At each margin of the crest there is a low minor cusp forming part of a circlet of similar cuspules that encircles about three-quarters of the crown's margin (Fig. 22B, b). The whole occlusal surface slopes downwards towards the presumed lingual side of the tooth. It is at the lowest point of the crown that the circlet of cuspules is interrupted. The bone of attachment is flared away from the vertical axis of the tooth on this lower side. There are three type III teeth, whose longest horizontal axes measure 9·5, 9·0 and 5·5 mm respectively.

On the basis of tooth outline in *Alestes macrolepidotus* and *Colossoma bidens* we would suggest that teeth of type II are from the midline of the jaw (that is, the first tooth in the row of each premaxilla), those of type III are next in position and are followed by teeth of type I. On this reckoning, *S. lepersonnei* would have had at least six teeth in the inner row of the upper jaw.

Our reconstructed arrangement of premaxillary teeth in this species (Fig. 22B, C) would, therefore, give an outer row of stout, functionally unicuspid but morphologically tricuspid teeth and an inner row of at least six molariform teeth with complex crown patterns of three different types. The basic crown pattern of each type is a single cusp and from one to three rows of minor cuspules.

Lower jaw. Outer row. Two types of presumed outer dentary teeth are recognizable (Figs 23A and 24).

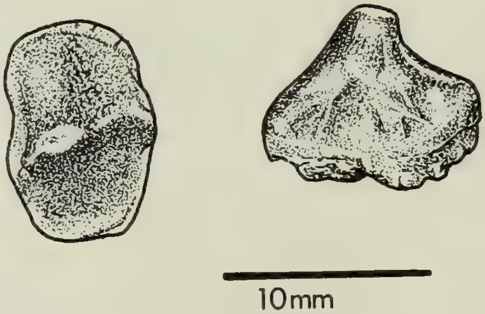

FIG. 24. *Sindacharax lepersonnei.* Dentary tooth from outer row, possibly the median tooth of this row (see text, p.103). (Paratype lot RG.17.600.)

In one (Fig. 23A) the outline of the occlusal surface is roughly cardiform, but without the median depression of a stylized heart. There is a single large, compressed and conical cusp whose peak lies at about the middle of the occlusal surface, but whose compressed shoulders extend to the margins. These shoulders are of unequal length. That on the side nearest the narrow end of the tooth is longer and slopes gently and gradually to merge with the crown's margin. The shorter shoulder at first slopes gently but then descends abruptly before merging with the margin. Both shoulders have, near their marginal extensions, a slight broadening of the cutting edge so that there is the semblance of a minor cuspule at that point. In other words, these teeth, like their counterparts in the upper jaw, are tricuspid. The presumed labial aspect of the crown is deeper than its lingual face, and there is a much deeper bone of attachment on that side as well, a condition common in the outer dentary teeth of several characoid species. There are six teeth of this type ; their longest horizontal axes are : 12·0 (f4) and 13·0 (f2) mm.

The second tooth type (Fig. 24) is represented by a single example (longest horizontal axis, 11·0 mm). It is basically similar to the other type of tooth, but has one face depressed into a broad and gentle concavity which distorts the cardiform outline characteristic of these teeth.

The position in the jaw cannot be established with any certainty for either tooth type. Since the outline of the first type (above) is not indented at any point it is less likely to be the medial tooth of the row. We argue thus because, in living characoids with an *Alestes* or *Colossoma* type of dentition, the median tooth is invariably recessed to accommodate the anterior face of the inner tooth. However, the second type of fossil tooth does have a very slight indentation on one aspect, and thus it may be the median tooth.

In their overall appearance and in their cusp pattern these teeth (and especially the second type) fairly closely resemble the antero-lateral outer row teeth from the dentary of *C. bidens*. Compared with the equivalent teeth in *Alestes* species, those of *S. lepersonnei* show a great reduction in cuspidation but have similarities in their outline shape and in the concave occlusal surface, a feature shared with the teeth of *C. bidens*.

Inner teeth. The basal outline of the teeth, of which only one type is recorded, is subcircular to oval. There is one large cusp with a well-defined cutting edge extending across the width of the base at an angle to its presumed lingual and labial margins (Fig. 23B). The posterior (i.e. lingual) aspect of the cusp is concave in lateral view, and the anterior face equally convex, so that the tip of the cusp is noticeably recurved. On the lingual aspect there is a narrow horizontal shelf that merges insensibly with the vertical face of the cusp.

Judged on the angle at which the cusp is orientated (see above, also Fig. 23B), left and right teeth are both represented in our sample. Also, since there is but one type of tooth referrable to the inner row, we conclude that there is only one inner tooth in each dentary.

The bone of attachment is deeply plicate, as it is in all other teeth of this species. The ventral plane of the tooth is, however, distinctly concave and is more markedly so on one side than the other.

There are nine presumed inner dentary teeth divisible into two groups, of five and four teeth each, on the basis of cusp orientation. The longest horizontal axis measures 8·0, 8·5, 9·0 (f3), 10·0, 11·0 (f2) and 11·5 mm.

In their gross morphology these teeth differ only slightly from their counterparts in *Alestes macrolepidotus*, although in that species the bone of attachment is much deeper and the cusp is rather less compressed. There is far less similarity with the inner teeth of the serrasalmines *Myletes* and *Colossoma*.

According to our identification of these various lower jaw teeth, *S. lepersonnei* would have had an outer row of stout, essentially unicuspid teeth with well-defined shearing edges and a small, horizontal surface behind the cusp. The first (or medial) tooth may have had this surface indented to receive the basal crown part of an inner tooth. The number of outer teeth cannot be determined, and there is little variation in the morphology of the outer teeth available to us. From the ventral outline of the bone of attachment we conclude that the teeth were attached to the dentary in exactly the same manner as are the outer teeth in extant characoids. Thus, each tooth would have a deep labial aspect and a shallow lingual one.

The inner dentary tooth row probably consisted of a single pair of stout unicuspids, one tooth on each ramus, differing little in their shape from those of many extant characoids.

Size. The teeth on which the taxon *S. lepersonnei* is based are large. Indeed, we have been unable to examine any extant serrasalmine or alestine characoid with teeth of a comparable size. In the largest *C. bidens* available to us, a now incomplete skeleton from the BM(NH) collections, the maximum length of the longest horizontal axis of the largest premaxillary outer tooth is 6·0 mm (cf. 13·0 mm in *Sindacharax*), of the largest premaxillary inner tooth 8·0 mm (cf. 15·0 mm), of the largest dentary outer tooth 8·0 mm (cf. 13·0 mm), and of the inner dentary tooth 6·0 mm (cf. 11·5 mm). The *C. bidens* skull measures 10·7 cm from the premaxillary symphysis to the basioccipital facet.

RELATIONSHIPS of *Sindacharax*, and the generic status of *Alestes deserti* Greenwood 1972. Taken in their entirety, the known teeth of *S. lepersonnei* do not resemble those of any extant species of African characoid. In many respects the closest resemblance, except for the inner premaxillary teeth, is with the dentition in certain New World serrasalmines, especially those of the genus *Colossoma*.

The only extinct African characoid for which dental details are available is *A. deserti* Greenwood, a species from the Pliocene of Wadi Natrun, Egypt.* (Fossil teeth of *Hydrocynus* are, of course, irrelevant to this discussion, as is the Eocene characoid from France whose teeth are certainly more like those of extant *Alestes* than those of either *A. deserti* or *S. lepersonnei* : Cappetta, Russell & Braillon 1972 ; also personal observations.)

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* Since this paper was completed, three further specimens of *A. deserti* teeth have come to light; all are from Kaiso, Lake Albert. Thus, not only is the range of this species extended geographically, but also temporally, into the range of *S. lepersonnei*. One of the new specimens, a third inner premaxillary tooth, is from Kaiso Village; the other two, a first inner premaxillary tooth (BM(NH) reg. no. P49205), and a worn tooth, possibly a third outer row dentary (P49206), are recorded merely as being from Kaiso, collected by Capt. C. R. S. Pitman, 1929.

The teeth of *A. deserti* depart quite markedly from those in all extant species of *Alestes*, and the Eocene species from France, particularly in having ridge-like cusps on teeth from the inner premaxillary series. In this respect the teeth of *A. deserti* resemble their counterparts in *S. lepersonnei*. There are also certain resemblances between some outer dentary teeth as well. On the other hand, no detailed similarities between inner premaxillary teeth in the two taxa could be found, and there are some differences in their outer premaxillary and outer dentary teeth. But, despite these dissimilarities and some similarity with the dentition of *A. macrolepidotus* (Greenwood 1972), the presence of cusp ridges across the inner premaxillary teeth in only *A. deserti* and *S. lepersonnei* is a characteristic that cannot be dismissed lightly.

As far as we can determine, the development of cusp ridges should be looked upon as a derived character state, and one coordinate with the cusp patterns found in extant *Alestes* species (see Greenwood 1972, for further discussion). This in turn leads us to consider whether or not *A. deserti* should be removed from the genus *Alestes* and treated as a taxon cognate with *Sindacharax*, and whether the two taxa should be placed in a suprageneric category distinct from the alestines.

The dental similarities of *S. lepersonnei* and *A. deserti* have been described, and the differences noted. What is perhaps significant here is the fact that in one of the differences, in the first dentary tooth, *A. deserti* resembles *Colossoma bidens*, and that the other may be fallacious and due to a misidentification of the position occupied by the tooth concerned in *A. deserti*, or for that matter in *S. lepersonnei*. We say this because the presumed outer premaxillary tooth in *A. deserti* closely resembles the presumed inner premaxillary tooth of type III in *S. lepersonnei*. These, the major dental differences separating *S. lepersonnei* and *A. deserti*, may be expressed in another way, namely that neither difference links *A. deserti* more closely with the genus *Alestes*, and that both have features that are reflected in the dentition of *Sindacharax* (compare Figs 22–24 with Greenwood 1972 : plate 1, figs 2–8).

Taking all these factors into account we therefore conclude that the several shared dental specializations found in *S. lepersonnei* and *A. deserti* indicate a closer relationship between the species than exists between *A. deserti* and any other species of the genus *Alestes*. *Alestes deserti* is accordingly now placed in the genus *Sindacharax*.

Any possible relationship between *Sindacharax* and certain elements, for example *Myletes* and *Colossoma*, of the serrasalmine lineage (now confined to the New World) is, of necessity, based on close resemblances in the outer teeth of these taxa (see pp. 100 and 102). The widespread occurrence of multicuspid outer teeth in the Characoidei suggests that the reduced cuspidation seen in serrasalmines and in *Sindacharax* is a derived condition, and therefore one possibly indicative of relationship between them. This assumption should not be construed as contradicting Roberts' (1967) thesis that unicuspid teeth are primitive in characoids. The teeth in *Sindacharax* and the serrasalmines are either basically tricuspid (with the median cusp hypertrophied) or of a unicuspid type that is no more like the presumed primitive kind (e.g. as in *Hoplias* or *Salminus*) than are the unicuspids of *Hydrocynus* (Roberts 1967).

Our thoughts on the problem of relationships between the serrasalmines and *Sindacharax* lead us to wonder whether perhaps *S. lepersonnei* and *S. deserti* are the last traces of an Old World serrasalmine lineage, a line that deviated from its New World relatives in having transversely multicuspid inner premaxillary teeth.

III. ANNOTATED LIST OF THE FISH REMAINS

The two new taxa from this collection, *Lates rhachirhinchus* (Centropomidae) and *Sindacharax lepersonnei* (? Characidae) are fully described on pp. 74–98 and 99–104 respectively. In this part of the paper only the number and kinds of skeletal parts from these two species are listed for any site.

Other fish remains (catfishes, a lungfish, possibly a cichlid and a mormyroid) are, in contrast with the *Lates* specimens, rather poorly represented in terms of both the number and variety of bones preserved. Geographically, however, most of these taxa are widely distributed within the area under consideration.

Identifying fishes from such fragmentary remains as these is not a simple task, and often cannot be carried with any confidence beyond the generic level. An important factor here is the ironical one that we generally had available a greater number of fossil specimens than of skeletal preparations from living species. Thus it is difficult to determine the range of interspecific variability for the extant species, and therefore to evaluate the significance of apparent morphological differences between them and the fossils. It follows, too, that we had no yardstick against which to measure possible intraspecific or intrapopulational variability amongst the fossils.

Much of the fossil catfish material consists of damaged fin spines. When identifying these we have used characters of ornamentation (ridges, tubercles, serrations, etc.) on the spine itself, and in the case of pectoral spines the morphology of the complexly folded articulatory proximal end. To a lesser degree, the proximal end of the dorsal fin spine also yields diagnostic characters. Among living catfishes these different features seem to be reliable for identification at the generic level, and in the case of mochokid pectoral spines even at the species-group level. The vertebral column, excluding the rarely preserved Weberian apparatus, yields fewer characters, and these are only reliable at a familial or higher level. The few syncranial bones preserved proved to be of little diagnostic value because of the damage they had sustained.

In the list that follows, the sites are grouped into three geographical subregions, viz. the Sinda-Mohari area (area 3 in Gautier's (1970) map, fig. 1), the Lake Albert and Nyamavi areas (1 and 2 in Gautier's map), and the Lake Edward and Upper Semliki areas (5 and 6 in Gautier's map). The entire region covered is thus essentially that lying between the northern end of Lake Edward and the south-western end of Lake Albert.

Sinda-Mohari Area

SINDA-MOHARI, POINT 15. Kabuga Formation (Lower Miocene).

Protopterus sp. Part of a left mandibular tooth plate and its associated cartilage is the sole representative specimen of this genus. In its morphology, the fossil compares closely with the equivalent tooth plate in living *P. aethiopicus*.

Auchenoglanis sp. A damaged proximal end from a left pectoral fin spine is referred to this genus with certainty, and a fragment of neurocranial bone is thought to be from an *Auchenoglanis*.

Clarotes sp. A fragment from the anterior part of the left frontal agrees in almost all details with that region of the bone in extant *C. niloticus*.

? Bagridae or Clariidae. A piece of centrum, showing the typical antero-posterior compression seen in the first free centrum of *Bagrus*, and in the anterior abdominal centra of clariid fishes, cannot be identified further.

Part of a fin spine (compressed and with serrations on one face only) may be a fragment of pectoral spine from a *Synodontis*. Its linear and somewhat sinuous ornamentation is like that in extant *Synodontis*, as is its generally compressed form.

Unidentifiable catfishes. Four fragments of fin spines (one definitely a dorsal spine) cannot be identified to family.

Lates, probably *L. rhachirhinchus*. Centropomids are not well represented, there being only one specimen of a first vertebra, one of a posterior abdominal vertebra and a gill raker. The morphology of the first vertebra is like that of *L. rhachirhinchus* (see p. 91).

OUTCROP NO. L98, RG2527–497. Right bank of the Mohari river. Mohari Beds (Lower Miocene).

Lates cf. *L. rhachirhinchus*. Two first vertebrae and a third vertebra all show features of these elements in *L. rhachirhinchus*, see p. 91. But since the specimens are damaged, the identification is considered to be a tentative one.

Auchenoglanis sp. The proximal, that is articular, end and about the proximal half of a dorsal fin spine is referred to this genus, as is another specimen (more incomplete) of a dorsal spine (the articular end and spine base only).

Synodontis sp. The articular head and the base of a pectoral spine (left) is referred to this genus.

Unidentifiable catfishes. Seven fragments of spines (from both dorsal and pectoral fins) are definitely from catfishes but cannot be identified further.

Sindacharax lepersonnei. The 4 teeth (1 outer premaxillary, 1 outer and 2 inner dentary) from this site constitute one of the earliest records for *S. lepersonnei*. As far as we can determine, there are no morphological differences between these teeth and those from later (earlier Pleistocene) deposits ; see pp. 110–114. The tooth from the outer row of the dentary is of the type 1 tooth described on p. 103.

ONGOLIBA BONE BEDS. (Material collected by de Heinzelin from Ongoliba in 1957 is included here.) Ridge 1, basal Sinda Beds (? earlier Pleistocene ; see p. 74).

Synodontis sp. One almost complete but slightly damaged dorsal fin spine is definitely referable to this genus, while 11 fragments of dorsal and pectoral fin spines are probably also referable to this taxon.

Siluriformes, indeterminable. One damaged centrum (30 mm wide), from the anterior abdominal part of the vertebral column, resembles comparable elements in extant members of the Bagridae and could well be from a *Bagrus* species.

Lates rhachirhinchus is well represented by 117 specimens including 13 from the skull, 9 jaw bones and 9 specimens of bones from the suspensorium. The vertebral column is represented by 9 first vertebrae, 13 third, 15 (and possibly 2 others) of the fourth or fifth vertebra, 2 sixth, 2 seventh and 44 posterior abdominal and caudal vertebra. Much of the syncranial material is included amongst the paratypical specimens (see p. 74).

Some indication of the size of the fishes preserved may be gained from the following measurements :

First vertebrae : breadth of anterior face in largest specimen *c* 37 mm, and in the smallest 14·0 mm.
Third vertebrae : breadth of anterior face in largest specimen 51·0 mm, and in the smallest 20·0 mm.
Fourth–fifth vertebrae : breadth of anterior face in largest specimen 55·0 mm, and in the smallest 16·0 mm.

The caudal and posterior abdominal vertebrae are from fishes in a similar size range.

SINDA-MOHARI, POINT 1, RIDGE 1. Derived blocks and fossils from the Ongoliba Bone Bed (? earlier Pleistocene ; see p. 74).

? *Synodontis* sp. Three pieces of fin spine are almost certainly referable to this genus.

Clariidae. A fragment of left frontal, comprising half of the fontanelle, part of the anterior interfrontal suture, a little of the bone lateral to the fontanelle, and the anterior angle of the bone, is typically clariid in its morphology, and does not resemble the frontal in any other family of extant African catfishes. This specimen is one of the few near-definite remains of a clariid fish found amongst the material from Sinda-Mohari, although some of the small neurocranial fragments from these deposits could be from fishes of this family. It is surprising that no pectoral fin spines nor, for that matter, any other skull fragments were recovered (but see p. 112).

Lates rhachirhinchus is well represented by 6 neurocranial fragments, 4 pieces of dentary, 1 premaxilla, 6 bones from the suspensorium, 1 gill raker and a total of 75 vertebrae (5 first vertebrae, 10 third, 7 fourth or fifth vertebrae, 2 ? sixth and 1 ? seventh vertebrae, and 50 posterior abdominal and caudal elements).

As an indication of the size range of *L. rhachirhinchus* represented at this site the following measurements are relevant :

First vertebrae : breadth of anterior face in the largest specimen 23·0 mm ; in the smallest 6·8 mm.
Sixth vertebrae : breadth of anterior face 52·0 mm, length of centrum 36·0 mm.

The caudal vertebrae indicate that smaller fishes were also present.

SINDA-MOHARI, POINT 2. Near Ongoliba ; as for Point 1, see above (Ongoliba Bone Bed ; ? earlier Pleistocene).

Clarotes sp. Two fragments of pectoral spines, both right, are referred to this genus, and closely resemble those of the *Clarotes* species from Point 10 (see p. 000). Some possible *Clarotes* vertebrae are mentioned below.

Auchenoglanis sp. The genus is represented by the proximal ends of 2 pectoral spines (1 left and 1 right from fishes of different sizes), and by a fragment from the distal end of a pectoral spine. In addition, the proximal end of another spine is tentatively referred to this taxon. The morphology of the articular head of the spine in this specimen does differ from that in the others, as does the ornamentation visible on the spine itself. Nevertheless, its overall morphology is closer to that of an *Auchenoglanis* pectoral spine than to that of any other genus.

Synodontis sp. Nineteen pectoral spines (9 left, 10 right), mostly comprising the articular head and proximal part of the spine, are referred to *Synodontis*. Judged on the ornamentation of these spines, only one species is represented in this material ; it appears to be identical with 'species A' from Point 10 (see p. 000). Eight smaller spine fragments should probably be referred to this genus, but no specific identification is possible.

Also identified as being derived from a *Synodontis* species are 17 dorsal fin spines. Like the pectoral spines, these are mostly damaged specimens comprising the proximal part of the spine and its anterior region. Thirteen of the spines have a serrated anterior margin, with the serrations distinct and prominent, and a smooth posterior face at least proximally. In these characteristics, the spines resemble those of 'species A' from Point 10. The remaining 4 spines have a sharp, keel-like anterior margin and serrations on the posterior face, thus resembling specimens referred to 'species B' from Point 10 (see p. 000 below).

Two small fragments are probably from the [illegible] of a dorsal spine, and 95
is impossible to tell from
ones cannot be identified
wo taxa are represented,
odontis. Five vertebrae
(2 of which show the antero-posterior compression typical of the first free vertebra in certain catfishes) would seem to be from a bagrid, and are very tentatively identified as being from a species of *Clarotes*.

letin of the British Museum (Natural History) Geology 26 (3).

The missing page references on page 109 are to page 111.

Lates rhachirhinchus. Specimens from this site cover a fairly wide spectrum of skeletal parts and a wide size range of individuals. Vertebrae are particularly well represented (313 specimens).

The skull is represented by 3 vomers and 8 basioccipitals, the jaws and suspensorium by 2 articulars, 1 quadrate, 1 dentary and 6 premaxillae, not including some fragments from the dentigerous arm of that bone, and the branchial skeleton by 16 gill rakers. One fragment can definitely be identified as part of a scapula, and another is tentatively identified as being part of an extrascapula. One large fin spine is provisionally referred to this species because of its size.

The vertebrae are identified as follows :

First : 24 specimens. Breadth of anterior face in largest specimen 60 mm, and in the smallest 8·0 mm.

Siluriformes, indeterminable. One damaged centrum (30 mm wide), from the anterior abdominal part of the vertebral column, resembles comparable elements in extant members of the Bagridae and could well be from a *Bagrus* species.

Lates rhachirhinchus is well represented by 117 specimens including 13 from the skull, 9 jaw bones and 9 specimens of bones from the suspensorium. The vertebral column is represented by 9 first vertebrae, 13 third, 15 (and possibly 2 others) of the fourth or fifth vertebra, 2 sixth, 2 seventh and 44 posterior abdominal and caudal vertebra. Much of the syncranial material is included amongst the paratypical specimens (see p. 74).

Some indication of the size of the fishes preserved may be gained from the following measurements :

First vertebrae : breadth of anterior face in largest specimen *c* 37 mm, and in the smallest 14·0 mm.
Third vertebrae : breadth of anterior face in largest specimen 51·0 mm, and in the smallest 20·0 mm.
Fourth–fifth vertebrae : breadth of anterior face in largest specimen 55·0 mm, and in the smallest 16·0 mm.

The caudal and posterior abdominal vertebrae are from fishes in a similar size range.

SINDA-MOHARI, POINT 1, RIDGE 1. Derived blocks and fossils from the Ongoliba Bone Bed (? earlier Pleistocene ; see p. 74).

? *Synodontis* sp. Three pieces of fin spine are almost certainly referable to this genus.

Clariidae. A fragment of left frontal comprising half of the fontanelle, part of
the anterior interfrontal suture,
anterior angle of the bone, is t
semble the frontal in any other
is one of the few near-definite r
from Sinda-Mohari, although s
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spines nor, for that matter, any other skull fragments were recovered (but see p. 112).

Lates rhachirhinchus is well represented by 6 neurocranial fragments, 4 pieces of dentary, 1 premaxilla, 6 bones from the suspensorium, 1 gill raker and a total of 75 vertebrae (5 first vertebrae, 10 third, 7 fourth or fifth vertebrae, 2 ? sixth and 1 ? seventh vertebrae, and 50 posterior abdominal and caudal elements).

As an indication of the size range of *L. rhachirhinchus* represented at this site the following measurements are relevant :

First vertebrae : breadth of anterior face in the largest specimen 23·0 mm ; in the smallest 6·8 mm.
Sixth vertebrae : breadth of anterior face 52·0 mm, length of centrum 36·0 mm.

The caudal vertebrae indicate that smaller fishes were also present.

SINDA-MOHARI, POINT 2. Near Ongoliba ; as for Point 1, see above (Ongoliba Bone Bed ; ? earlier Pleistocene).

Clarotes sp. Two fragments of pectoral spines, both right, are referred to this genus, and closely resemble those of the *Clarotes* species from Point 10 (see p. 000). Some possible *Clarotes* vertebrae are mentioned below.

Auchenoglanis sp. The genus is represented by the proximal ends of 2 pectoral spines (1 left and 1 right from fishes of different sizes), and by a fragment from the distal end of a pectoral spine. In addition, the proximal end of another spine is tentatively referred to this taxon. The morphology of the articular head of the spine in this specimen does differ from that in the others, as does the ornamentation visible on the spine itself. Nevertheless, its overall morphology is closer to that of an *Auchenoglanis* pectoral spine than to that of any other genus.

Synodontis sp. Nineteen pectoral spines (9 left, 10 right), mostly comprising the articular head and proximal part of the spine, are referred to *Synodontis.* Judged on the ornamentation of these spines, only one species is represented in this material ; it appears to be identical with 'species A' from Point 10 (see p. 000). Eight smaller spine fragments should probably be referred to this genus, but no specific identification is possible.

Also identified as being derived from a *Synodontis* species are 17 dorsal fin spines. Like the pectoral spines, these are mostly damaged specimens comprising the proximal part of the spine and its anterior region. Thirteen of the spines have a serrated anterior margin, with the serrations distinct and prominent, and a smooth posterior face at least proximally. In these characteristics, the spines resemble those of 'species A' from Point 10. The remaining 4 spines have a sharp, keel-like anterior margin and serrations on the posterior face, thus resembling specimens referred to 'species B' from Point 10 (see p. 000 below).

Two small fragments are probably from the distal part of a dorsal spine, and 95 others are tentatively referred to *Synodontis*, although it is impossible to tell from which fin spine they are derived.

Unidentifiable catfishes. Four pieces of skull roofing bones cannot be identified further. Differences in the ornamentation suggest that two taxa are represented, and that one may be *Auchenoglanis* and the other *Synodontis.* Five vertebrae (2 of which show the antero-posterior compression typical of the first free vertebra in certain catfishes) would seem to be from a bagrid, and are very tentatively identified as being from a species of *Clarotes.*

Lates rhachirhinchus. Specimens from this site cover a fairly wide spectrum of skeletal parts and a wide size range of individuals. Vertebrae are particularly well represented (313 specimens).

The skull is represented by 3 vomers and 8 basioccipitals, the jaws and suspensorium by 2 articulars, 1 quadrate, 1 dentary and 6 premaxillae, not including some fragments from the dentigerous arm of that bone, and the branchial skeleton by 16 gill rakers. One fragment can definitely be identified as part of a scapula, and another is tentatively identified as being part of an extrascapula. One large fin spine is provisionally referred to this species because of its size.

The vertebrae are identified as follows :

First : 24 specimens. Breadth of anterior face in largest specimen 60 mm, and in the smallest 8·0 mm.

Third : 25 specimens. Breadth of anterior face in largest specimen 54 mm, and in the smallest 9·0 mm.

Fourth or fifth : 24 specimens. Breadth of anterior face in the largest specimen 53 mm, and in the smallest 6·0 mm.

? Sixth : 3 specimens. Breadth of anterior face in the largest specimen 50 mm, and in the smallest 13 mm.

? Seventh : 10 specimens. Breadth of anterior face in the largest specimen 45 mm, and in the smallest 8·0 mm.

Altogether there are 227 posterior abdominal and caudal centra of which 125 are classified as the elongate posterior caudal type. The measurements of the largest and smallest centra in the latter group (i.e. elongate type) are : breadth of anterior face 19 mm and 4 mm ; length 23 mm and 8 mm ; width 14 mm and 3 mm. Measurements of the former group are : breadth of anterior face 49 mm and 8 mm ; length 40 mm and 8 mm ; width 48 mm and 6 mm.

? Cichlidae. Four vertebrae are tentatively identified as being derived from cichlid fishes ; from their size, it is thought that the fishes represented were in the size range of 30–35 cm standard length, that is, within the adult size range of several living *Sarotherodon* species. Two of the centra may be from third vertebrae because there appear to be the remains of the base of the stout apophysis which is developed from that centrum in present-day *Sarotherodon* ; also the rib facet of these specimens resembles that on the third vertebra in extant *S. niloticus*. The two other centra are identified as those of caudal vertebrae.

SINDA-MOHARI, POINT 3. Western slope of Ridge 2 ; fossils derived from the Ongoliba Bone Bed (? earlier Pleistocene).

? *Synodontis* sp. A small piece of dorsal fin spine is probably from a member of this genus.

Lates rhachirhinchus. The species is rather poorly represented by a fragment of the angulo-articular, a vomerine tooth patch and 6 vertebrae. Specific identification is based partly on the shape of the angulo-articular (seep. 88) and partly on the morphology of the third, fourth or fifth and ? seventh vertebrae (see p. 92).

SINDA-MOHARI, POINT 4. Right bank of the eastern branch of the Kabuga valley ; fossils collected on the slopes, which are derived from the basal Sinda Beds (Zone A ; ? earlier Pleistocene).

? *Clarotes* sp. Three fragments of skull roofing bones are ornamented with densely arranged, high and bluntly conical tubercles, very similar in appearance to those of extant *Clarotes* species.

? *Auchenoglanis*. Again, our tentative identification is based on similarities between the ornamentation on the two fragments of skull bone and skull bones in living species.

Lates rhachirhinchus. The species is represented only by vertebrae, namely : a first vertebra, a third, a sixth and a caudal vertebra. All are from fishes of *c* 45 cm standard length. The morphology of the first and third vertebrae is characteristic of *L. rhachirhinchus*.

SINDA-MOHARI, POINT 5. Ridge 1. On slope towards the Kabuga river; reworked material derived from the lowest Bone Beds and the Sinda Beds, Zone A (? earlier Pleistocene).

Lates rhachirhinchus. Although poorly represented at this site by 1 palatine and 1 first vertebra, the palatine bone is of considerable interest (see p. 85).

SINDA-MOHARI, POINT 10. Ridge 1, northern part. Material from a profile 2·5 and 3·1 m above the interface between the Sinda Beds and the Mohari Formation (Ongoliba Bone Bed; ? earlier Pleistocene). In many respects, including the number of fish species represented, this is the most important site in the Sinda-Mohari area.

Sindacharax lepersonnei (see p. 99). This peculiar characoid is represented by 6 fairly well-preserved teeth (2 from the lower jaw and 4 from the premaxilla), and 3 fragments of teeth.

? *Clarotes* sp. No material is definitely assignable to this genus, but the following are tentatively identified as *Clarotes* remains:

(i) A right angulo-articular.
(ii) Three damaged dorsal fin spines, comprising the articular head and a little of the spine itself.
(iii) Two fragments of dorsal fin spine, distal end.
(iv) Four pieces of skull roofing bone identified on the basis of the ornamentation.
(v) Three (2 left and 1 right) extremely damaged pectoral fin spines, comprising the articular head and part of the spine.

? *Auchenoglanis.* Like the *Clarotes* material, that referred to *Auchenoglanis* is only tentatively so assigned:

(i) Two dorsal fin spines, comprising the articular head and the proximal part of the spine.
(ii) Four (2 left and 2 right) pectoral spines (damaged), comprising the articular head and the proximal sixth to half of the spine.
(iii) Three small fragments of skull roofing bones identified on the basis of their ornamentation.

? Bagridae. One anterior abdominal vertebra (width of centrum *c* 2·1 cm), and a specimen of the first free centrum posterior to the fused centra associated with the Weberian apparatus (width *c* 2·8 cm), are thought to be from a bagrid fish. The first centrum closely resembles that in extant *Bagrus docmac.*

Synodontis spp. The genus is best represented by numerous fin spines, amongst which two types of ornamentation can be recognized, suggesting the presence of two species.

Twenty-five specimens of *pectoral spines* (10 left, 15 right), each comprising the articular head of the spine and, in most cases, part of the spine as well, have both the anterior and posterior faces serrated. The anterior serrations are conical and extend to the base of the spine. The posterior serrae are flattened and dagger-like, and extend, or almost extend, to the base of the spine. This ornamentation type will be referred to as 'Species A' (see p. 109). In addition to this material there are three spines of 'Species A' lacking the articular head.

Eight pectoral spines (5 left, 3 right), fragmented like those described above, are referred to as 'Species B'. In these the serrae on the anterior face are smaller, finer and more closely spaced. Serrae on the posterior aspect of the spine are like those on the anterior face.

Thirty-two fragments from the proximal part of the pectoral spine are tentatively referred to *Synodontis*, but cannot be assigned to a particular 'species'.

The *first pungent dorsal fin spine* is also separable into two types. In 8 specimens, referred to as 'Species A', the posterior face is smooth, while the anterior face carries stout, subconical serrae. The second type ('Species B') is represented by a single specimen in which the anterior face of the spine is produced into a sharp ridge, and there are some serrations on the posterior face, beginning at a point about one-third along the length of the spine.

In addition to these specimens, 17 other and more fragmentary spines are tentatively referred to *Synodontis*, as are 180 small fragments mostly from pectoral spines but including some thought to be from dorsal spines.

Unidentifiable catfishes. Several hundred small pieces of fin spines, probably from bagrid and mochokid catfishes, cannot be identified more precisely.

Lates rhachirhinchus. By far the greatest number and anatomical variety of specimens are from this site. There are 41 specimens of neurocranial fragments, 7 maxillae, 51 premaxillae, 93 fragments of dentary, 55 bones or fragments of bones from the palatoquadrate arch (including one palatine bone, see p. 85), a fragment of scapula, part of what is thought to be an epihyal, 65 gill rakers and 9 fragments probably from branchiostegal rays. In addition there are 38 first vertebrae, 35 third, 28 fourth or fifth, 4 ? sixth and 7 ? seventh vertebrae, together with 172 posterior abdominal and caudal vertebrae, 8 specimens of the fused first ural and first preural centra, some with remains of hypurals still present, and a single isolated hypural. The holotype of the species, a vomer, is from this site. The material examined is derived from a wide size range of individual fishes; the largest is estimated to have had a standard length of *c.* 150 cm, i.e. within the size range of extant *L. niloticus*.

SITE 59. Downstream of Mtoto ya Ongoliba (Kabuga river). Probably derived from Sinda Beds.

Protopterus sp. A fragment of mandibular tooth plate is the only specimen referable to this taxon.

? Clariidae. A fragment of dentary (including part of the alveolar surface) most closely resembles that region of a clariid dentary slightly anterior to the hind end of its dentigerous surface, i.e. where the body of the bone begins to narrow. The pattern of the dentigerous surface suggests a dense felt of small teeth. A piece of skull roofing bone also is tentatively referred to this family. If our identifications are correct, these two specimens together with the frontal from Point 1 (p. 108) are the only clariid remains from the Sinda-Mohari region, a surprising state of affairs since clariid remains are usually the commonest fossils in Quaternary African lake and river deposits.

? Bagridae. Part of a dentary is tentatively identified as coming from a bagrid fish. The alveolar surface indicates that there was a fine felt of closely packed and small teeth. Although the horizontal curvature of this bone is like that in extant *Bagrus* species, its ventral profile has the form of a broadly rounded ridge, not a sharp one as in *Bagrus*.

SURFACE FINDS NO. L145, RG2628–531.* Sinda river, probably derived from basal Sinda Beds.

Sindacharax lepersonnei. The species is represented by 4 teeth, viz. 1 from the outer premaxillary row, 2 from the outer and 1 from the inner row of dentary teeth.

SURFACE FINDS NO. L145, RG2638–531(B). Left bank of Sinda river, probably derived from basal Sinda Beds.

Lates cf. *L. rhachirhinchus*. The only *Lates* material from this site consists of vertebrae, viz. 4 first, 3 third, 4 fourth or fifth, 1 ? seventh and 10 posterior abdominal and caudal elements. Judged on the characteristics of the first, third and fourth or fifth centra, the species is probably *L. rhachirhinchus*.

SURFACE FINDS NOS L146 and 156, RG2448–531(C). Left bank of Sinda river, probably derived from basal Sinda Beds.

Sindacharax lepersonnei. The species is represented by a total of 4 teeth, viz. 2 outer premaxillary teeth (one merely an enamel cap and therefore probably a replacement tooth), 1 inner premaxillary tooth (probably median in position) and 1 tooth from the outer series of the dentary.

Lates sp. probably *L. rhachirhinchus*. Four first vertebrae and one specimen of the fused first preural and ural centra are from a *Lates*. Three of the first vertebrae show the typical characteristics of this element in *L. rhachirhinchus*, but the fourth specimen is much compressed antero-posteriorly, especially over its ventral half. In this respect, it differs from all species and specimens of *Lates* we have examined.

OUTCROP NO. L100, RG2546–498A. Right bank of Mohari river, base of Sinda Beds.

Lates sp. possibly *L. rhachirhinchus*. The one first vertebra from this site is damaged but shows characteristics of that element in *L. rhachirhinchus* (p. 91). The posterior abdominal centrum shows no diagnostic features, but the relatively elongate caudal centrum is like that in *L. rhachirhinchus*.

OUTCROPS NOS L145 and L156, RG2650–531(C). Surface finds, base of Sinda Beds.

? Bagridae. Four damaged centra with the typical cancellous pattern and the overall morphology of caudal vertebrae in the genus *Bagrus* are referred, tentatively, to this family.

Lates rhachirhinchus. Only vertebrae of this species are recorded, and comprise : 19 first, 10 third, 13 fourth or fifth, 1 ? sixth, 2 ? seventh and 165 posterior abdominal and caudal vertebrae.

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* This and subsequent RG numbers are locality numbers and not specimen register numbers.

? Cichlidae. A damaged posterior abdominal vertebra closely resembles comparable elements in the extant species *Sarotherodon niloticus*, and is referred, tentatively, to this family.

Outcrops nos 145 and 156, RG2651–531(C). Left bank of Sinda river, base of Sinda Beds, Zone A (? earlier Pleistocene).

Lates rhachirhinchus. The species is represented by 5 incomplete dentaries (3 left, 2 right). The toothed area and the large lateral line canal pores are typical of *L. rhachirhinchus* (see p. 88).

Outcrops nos 145 and 156, RG2653–531(C). Left bank of Sinda river, base of Sinda Beds.

Sindacharax lepersonnei. This site has yielded the greatest number and variety of *S. lepersonnei* teeth, and is the source of all paratypical material (see list on p. 99).

Outcrops nos 145 and 156, RG2659–531(C). Site details as above.

Clarotes sp. A left pectoral fin spine (comprising the articular head and part of the spine), 2 fragments from the distal end of pectoral spines and a dorsal fin spine (proximal end) are placed in this genus on the basis of their ornamentation and on the morphology of their proximal, articular surfaces.

Synodontis sp. Five dorsal fin spines (proximal end) and 13 damaged pectoral spines (7 left, 6 right comprising the articular heads and proximal part of the spine) are identified as being from *Synodontis* ; 5 proximal fragments of pectoral spines and 58 fragments of fin spines (pectoral and dorsal) are tentatively referred to this genus.

Outcrops nos 145 and 156, RG2661–531(C). Site details as above.

Sindacharax lepersonnei. Two teeth, a lower inner and an upper inner.

Synodontis sp. A damaged left pectoral spine (proximal end) and 8 fragments of pectoral spines are tentatively referred to this genus.

Outcrops nos 145 and 156, RG2663–531(C). Site details as above.

Lates rhachirhinchus. The species is represented by three bones, viz. a basioccipital (depth of facet for first vertebra 14·0 mm), a large fragment of the left anguloarticular showing the typical morphology for this species (p. 98) and a left premaxilla, damaged but with the specific characteristics preserved. A fourth specimen is tentatively identified as part of a centropomid ceratohyal.

Locality unrecorded, RG2668–531(C). No other data.

Synodontis sp. Two dorsal fin spines (proximal ends only), 2 pectoral fin spines (both left, consisting of the articular head and proximal part of the spine) and 3 fragments from the distal ends of pectoral spines are referred to this genus.

Mbovo Outcrop no. Liii, RG2572–511. Sinda Beds, Zone B (Lower Pleistocene, Villafranchian).

Lates sp. The only specimen of this genus is a fragment of frontal still deeply embedded in a matrix that has proved resistant to chemical cleaning. Although the bone is certainly from a centropomid fish, it is not possible to determine from which species of *Lates* it was derived.

OUTCROP NO. L162, RG2680–545. Right bank of Sinda river, Sinda Beds, Zone B (Lower Pleistocene, Villafranchian).

Lates sp. No species-diagnostic characters are obtainable from the one posterior abdominal and the one caudal centrum preserved at this site.

SINDA-MOHARI, POINT 6. Right bank of the Sinda river near the Semliki scarp, Sinda Beds, Zone C (Lower Pleistocene and younger than beds of Zone B).

Clarotes sp. The articular head and approximately the basal third of a left pectoral spine agrees in all morphological details with that spine in extant *Clarotes*.

Unidentifiable catfish. Part of a fin spine, probably from the pectoral fin, is certainly from a siluriform fish, but cannot be identified further.

Lates cf. *L. niloticus* and *L. rhachirhinchus*. Centropomid material from this site is of particular interest because, whenever diagnostic features are preserved, some specimens show greater similarity with the extant *L. niloticus* than with *L. rhachirhinchus*, the characteristic and unique species of earlier deposits. However, other bones do exhibit features that suggest *L. rhachirhinchus*. For example, the well-preserved angulo-articular shows in lateral view a shallow articular facet, contrasting with the deep facet of *L. rhachirhinchus*, and a posterior margin that does not rise steeply or incline anteriorly as it does in *L. rhachirhinchus*. Furthermore, the lateral-line canal underlying this surface is of the short, *L. niloticus* type (see p. 88). The three incomplete (1 left and 2 right) dentaries, on the other hand, have the relatively narrow dentigerous surface and the large lateral-line pores characteristic of *L. rhachirhinchus*. A fourth fragment of dentary is too incomplete to show any diagnostic features. The vertebrae are perhaps nearer the *L. rhachirhinchus* type than those of *L. niloticus*. An exceptional specimen is the only second vertebra recorded from the entire Sinda-Mohari area. It is virtually identical with its counterpart in *L. niloticus* ; indeed, it is nearer that than the second vertebra of *L. calcarifer*. Vertebral specimens comprise 1 second, 2 third, 1 fourth or fifth, 1 ? seventh and 2 posterior abdominal or caudal centra. Other *Lates* bones are part of a premaxilla (the dentigerous arm and therefore of no diagnostic value) and a pelvic fin spine. The latter, which comprises only the articular region and a short segment of the spine itself, is from a very large fish : the vertical depth of the spine and its articular surfaces is at least 2 cm since part is missing. It is difficult to draw any definite conclusions from these few specimens. Perhaps both a *L. niloticus*-like species and *L. rhachirhinchus* were present, or these bones may be from a third taxon which combined features of both species.

Lake Albert and Nyamavi areas

KARUGAMANIA BEDS (Lower Miocene). Collected by J. de Heinzelin.

Sindacharax lepersonnei. This taxon is represented only by a damaged type 1 tooth from the inner premaxillary series (p. 101).

Unidentifiable catfishes. A fragment of a strong fin spine, serrated on one face, is thought to be derived from a catfish.

Lates sp. A fragment of vertebra (centrum) is undoubtedly from a *Lates* but no specific identification is possible.

KARUGAMANIA BEDS (Lower Miocene), RG2279–445.

Lates sp. (probably *L. rhachirhinchus*). *Lates* remains from this site comprise an incomplete basioccipital, 2 specimens of a fourth or fifth vertebra, 3 of a ? sixth vertebra and 1 caudal element. The morphology of these abdominal vertebrae (especially the fourth or fifth) is virtually identical with that of comparable elements in *L. rhachirhinchus* from other localities (see pp. 107–115), and differs markedly from that in *L. niloticus* (or *L. niloticus*-like fossils). The caudal vertebra provides no diagnostic features.

KARUGAMANIA BEDS (Lower Miocene), RG2282–445.

? Mochokidae. A small portion of a fin spine is thought to be derived from a mochokid catfish.

KARUGAMANIA BEDS (Lower Miocene), RG2316–446, outcrop no. L48.

? Catfish. A large caudal vertebra (width of centrum 21·0 mm, depth 22·0 mm) is probably derived from a bagrid catfish.

NYAMAVI AREA, RG2485–490, outcrop no. L81 (Upper Miocene or Lower Pliocene).

? Bagridae. Three centra (respectively 29·0, 26·0 and 25·0 mm wide), probably from posterior abdominal vertebrae, are possibly from a bagrid species, but cannot be identified more precisely.

Lates sp. or spp. With only vertebral material available, it is difficult to be certain about the specific identity of the *Lates* preserved at this site. The two specimens of the third vertebra could be from either a *L. niloticus*-like fish, or from *L. rhachirhinchus*. The single specimen of a first vertebra seems to combine features of *L. rhachirhinchus* and features not found in that species or in any other *Lates* species living or extinct. The nature and pattern of the central trabeculae, and the shape of the 'saddle' separating the exoccipital facets, are *L. rhachirhinchus*-like. The centrum is noticeably narrowed antero-posteriorly over its ventral half, a feature seen in a few other fossils from this region (see p. 91) but not in extant *Lates*. Finally, the shape of the exoccipital facets is unlike that in any extant or extinct species.

NYAMAVI, outcrop no. L68, RG2395–464/1. Upper Nyamavi Beds, member VI (Lower Pleistocene).

Clarotes sp. Five pectoral fin spines (1 left and 4 right), each comprising the articular head and base of the spine, are referred to this genus on the basis of articular surface morphology. Nine fragments from the distal part of the spine are also identified as *Clarotes* on the basis of their ornamentation. A large part of the fused vertebral mass associated with the Weberian apparatus shows, in some respects, certain similarity with that element in *Clarotes*. But in other ways it is unlike this structure in any living African catfish group. Because of the specimen's incompleteness, it seems unlikely that a more positive identification can be made.

? *Auchenoglanis* sp. Part of a right quadrate is referred to this genus because it has the characteristic articular surface of extant *Auchenoglanis* species.

? *Synodontis* sp. A damaged pungent dorsal fin spine (comprising the articular base and about the proximal third of the spine) has a smooth posterior face, and the anterior face ornamented with small, fine tubercles more or less fused into a narrow ridge. In these respects it closely resembles one of the two types of *Synodontis* dorsal spine found in Lower Pleistocene beds of the Sinda-Mohari area (see p. 112). However, this specimen differs from the Sinda-Mohari species in having the small facets on its anterior face for the reduced first dorsal spine of a very different shape. Indeed, this shape was not encountered in any of the several extant *Synodontis* species we examined. For this reason our identification must be considered tentative.

NYAMAVI, RG2398–464/1. Upper Nyamavi Beds, member VI (Lower Pleistocene).

Clarotes sp. Five fragments of skull roofing bones are referred to this genus on the basis of their ornamentation.

NYAMAVI, outcrop no. L68, RG2406–464/1. Upper Nyamavi Beds, member VI (Lower Pleistocene).

Clarotes sp. A fragment of right operculum (upper third of the bone, including the articular facet) and 3 pieces of roofing bone are referred to this genus, the latter specimens with less certainty than the former.

NYAMAVI, outcrop no. L68, RG2398–464/1. Upper Nyamavi Beds, member VI (Lower Pleistocene).

Clarotes sp. Two articulars (1 left and 1 right but from different individuals) and 2 fragmentary basioccipitals (width across facet 13·0 and 14·0 mm respectively) are referred to this genus with certainty. Another fragment appears to be part of a *Clarotes* post-temporal bone.

Lates sp. Seven poorly preserved centra (probably from caudal or posterior abdominal vertebrae) are the only *Lates* remains, and cannot be identified to species.

Lake Edward and Upper Semliki areas

LAKE EDWARD, 1000–1500 m east of Ishango, outcrop no. L273, RG2741–608. Lake Edward Beds (Lower Pleistocene, Villafranchian).

? *Hyperopisus* sp. (Fig. 25). Four low-crowned and generally molariform teeth are very tentatively referred to this or some closely allied and extinct genus. The teeth could be derived from the parasphenoid or basihyal tooth plates. In all specimens the crown shows signs of wear, and in some there is an eccentric pit like that produced when wear destroys a single cusp. The teeth are subcircular in outline and there is a variation in their relative crown length, some being flatter, others more domed. The maximum widths of the four teeth are 5·0, 7·0, 7·5 and 9·0 mm respectively; it is estimated that they are derived from a large fish of *c* 75–100 cm standard length. Very similar teeth, also tentatively identified as being from *Hyperopisus*, are recorded from the Lower Pleistocene deposits at Kanyatsi, east of Ishango (Greenwood 1959). More certainly identifiable *Hyperopisus* teeth come from the Pliocene beds of Wadi Natrun, Egypt (Greenwood 1972).

KANYATSI, 20–25 m above lake level, outcrop no. L275, RG2761–617. Lake Edward Beds (Lower Pleistocene, Villafranchian).

Lates sp. A fragment of centrum, probably from an anterior abdominal vertebra; no specific characters are preserved.

Nyakavia Ravine, outcrop no. L283–285, RG2811–651. Lake Edward Beds (Lower Pleistocene, Villafranchian).

? *Synodontis* sp. A fragment from the proximal end of a dorsal fin spine, without the articular surfaces, is tentatively referred to this genus on the basis of its ornamentation (serrated posterior face ; anterior face probably keeled).

Lates cf. *L. niloticus*, and also possibly *L. rhachirhinchus*. The genus is relatively well represented by a number of vertebral centra including some which show specifically diagnostic features.

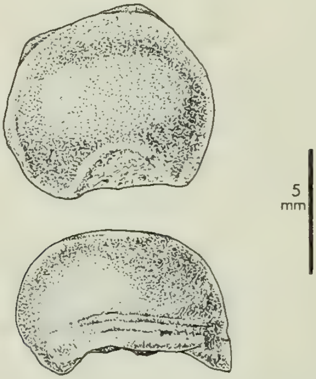

Fig. 25. ? *Hyperopisus* sp. Isolated tooth (basihyoidal or parasphenoidal) in (top) occlusal and (bottom) lateral views.

First vertebra : 2 specimens (one damaged, the other in good condition). These bones resemble the centrum found in *L. niloticus* although one specimen has a shorter ventral than dorsal length, in that way resembling the first vertebra of *L. rhachirhinchus* (see p. 91). The other specimen is identical to this vertebra in extant *L. niloticus*.

Second vertebra : 1 specimen. Closely resembling that of *L. niloticus*.

Third vertebra : 2 specimens. It is not possible to be certain about the specific identity of these bones. A third and much smaller specimen is also tentatively identified as a third vertebra.

Fourth vertebra : 1 specimen. Although damaged, it is possible to say that this centrum closely resembles its counterpart in *L. niloticus*.

Fifth vertebra : 2 specimens (one entire, the other badly damaged) ; both are like that vertebra in *L. niloticus*.

Sixth vertebra : 1 specimen from a much smaller fish than those from which the other specimens were derived. It is identical to the sixth vertebra in *L. niloticus*.

Caudal and posterior abdominal vertebrae : A total of 31 centra, of which 10 show the characteristic elongation and narrow waisted condition typical for *L. rhachirhinchus*.

The remaining specimens cannot be identified to species.

Ravine Kio, outcrop no. L288, RG2830–658. Lake Edward Beds (Lower Pleistocene).

Lates sp. The single, damaged specimen of a third vertebra and 5 poorly preserved caudal (or posterior abdominal) centra cannot be further identified.

Ishango Terrace, outcrop no. L298, RG2877–673. Upper Pleistocene.

Lates sp. One centrum, and the base of the right neural arch, of an abdominal vertebra, thought to be the eighth or ninth element in the series because of the size of its 'transverse process'. Specific identification is impossible.

Ishango Terrace, outcrop no. L298, RG2883–673A. Upper Pleistocene.

Lates sp. cf. *L. niloticus*. A damaged vertebra, thought to be a fifth abdominal, compares closely with that vertebra in extant *L. niloticus*. There is also the centrum of a caudal vertebra ; it cannot be specifically identified.

? *Sarotherodon*. Three centra (two posterior abdominal and a caudal) closely resemble those in a comparable-sized *S. niloticus* (Cichlidae). These bones are from a fish estimated to be about 30 cm standard length.

Lake Edward, 1000–1500 m east of Ishango, outcrop no. L302, RG2893–677. Lake Edward Beds (Lower Pleistocene).

? Centropomidae. A fragment of a fin spine is referred to this family because of its large size, presumably too large to be derived from a member of the Cichlidae.

Upper Semliki, upstream from Senga, on the right bank ; outcrop no. L315, RG2912–687. Lake Edward Beds (Lower Pleistocene).

Lates sp. One damaged centrum, probably caudal, still deeply embedded in an intractable matrix. Further identification is impossible.

Upper Semliki, RG2919–688. Site data and age as above.

Lates sp. The centrum of a third vertebra, for which no specific identification is possible.

Upper Semliki, 1000 m downstream from Senga ; outcrop no. L317, RG2925–690. Lake Edward Beds (Lower Pleistocene).

? Centropomidae. An almost complete dorsal fin spine is referred to this family because of its size.

Upper Semliki : Luamiti, outcrop no. L327–328, RG2944–693. Lake Edward Beds (Lower Pleistocene).

Clarotes sp. A fragment of a left pectoral fin spine, including the damaged articular head and the proximal third of the spine, is referred to *Clarotes* because of its ornamentation and the morphology of the articular head.

Upper Semliki, Mupanda, left bank, outcrop no. L328, RG2948–694. Lake Edward Beds (Lower Pleistocene).

Clarotes sp. A fragment from a right pectoral fin spine, including the articular head and the proximal part of the spine itself. The generic identification is based, principally, on the morphology of the articular head, but also on the ornamentation of the spine.

? Catfishes. Four fragments of vertebral centra from this site are thought to be from a catfish, but cannot be further identified.

IV. CONCLUSIONS

Generally it is impossible to identify fragmentary material such as this to the species level, mainly because the osteology of extant species is so poorly known that we cannot assess the diagnostic value of whatever characters are preserved in the fossils. Species like *Sindacharax lepersonnei* and *Lates rhachirhinchus* are exceptional, either because the structures involved (teeth) have been better studied or because the osteology of extant species is well known, as in *Lates*. Thus, it is quite likely that the other species represented in these collections, for example the several catfishes, may be equally distinctive when compared with their living congeners or with extinct species from other localities and times.

With this reservation in mind, however, it is still possible to compare this collection with those from later deposits in the Edward–Albert Rift (Greenwood 1959) and from contemporary or later deposits elsewhere in Africa (White 1926 ; Greenwood 1951, 1972, 1973b).

Except for *Sindacharax* the Miocene fish fauna of Sinda-Mohari has a typically basic Nile–Zaire facies, basic here implying that none of the endemic or specialized genera of these rivers is represented. In this respect it is akin to the Miocene fauna of Bled ed Douarah in Tunisia (Greenwood 1973b), that of the Miocene lake once occupying part of the Lake Victoria basin (Greenwood 1951), and the Pliocene fauna of Wadi Natrun, Egypt (Greenwood 1972) where *Sindacharax* was also present. The similarity can be carried forward in time to include the Pleistocene fishes of the Edward–Albert Rift (see pp. 106–119, and Greenwood 1959).

Sindacharax, apart from its occurrence in the Miocene and earlier Pleistocene of Sinda-Mohari and the Miocene of Lake Albert, is also known from the Pliocene of Wadi Natrun and Kaiso deposits of Lake Albert, where it is represented by a species differing in several dental characters and, seemingly, in reaching a smaller size (see p. 104 above, and Greenwood 1972). Furthermore, the relationships of this genus are apparently exceptional within the entire African freshwater fish fauna of Quaternary and Recent times (p. 105 above).

Some note must also be made of certain 'absentee' elements that might be expected to occur in the Sinda-Mohari fauna and which are absent also from the Miocene of Lake Albert ; see Table I. For example, there is no indication of any species of *Hydrocynus* or *Hydrocynus*-like fish (Characidae), although this genus was present in the nearby Lower Pleistocene deposits of Kanyatsi and the Pliocene of Egypt (Greenwood 1959, 1972). Catfishes of the family Clariidae are possibly represented by a single vertebra. Clariids are definitely present in the Miocene of Tunisia (Greenwood 1973b), the Pliocene of Egypt (Greenwood 1972) and in Middle Pleistocene deposits near Lake Edward. Interestingly, clariid remains are only doubtfully recorded from the basal Sinda Beds of the Sinda-Mohari area and the Lower Pleistocene of Kanyatsi (Lake Edward).

No member of the Cyprinidae, for example *Barbus* or *Labeo*, is represented in the Miocene of Sinda-Mohari nor, for that matter, in the Pleistocene beds of this area, but cyprinids are present at Wadi Natrun (two genera, Greenwood 1972) and probably Tunisia (Greenwood 1973b). It may be significant that the earliest record of a

TABLE I

Summary of species recorded from the three major areas discussed on pp. 106–119.*

	Lower Miocene	Pliocene or earlier Pleistocene (Basal Sinda Beds)	Lower Pleistocene
Sinda-Mohari	*Protopterus* sp.	*Protopterus* sp.	
	Sindacharax lepersonnei	*Sindacharax lepersonnei*	
	Synodontis sp.	*Synodontis* sp.	
	Auchenoglanis sp.	*Auchenoglanis* sp.	
	Clarotes sp.	*Clarotes* sp.	*Clarotes* sp.
	? Clariidae	? Clariidae	*Lates* sp. (cf. *L. niloticus*)
	Lates cf. *L. rhachirhinchus*	*Lates rhachirhinchus*	
		? Cichlidae	*Lates rhachirhinchus*
Lake Albert and Nyamavi	*Sindacharax lepersonnei*		? *Synodontis* sp.
	Lates sp.		? *Auchenoglanis* sp.
	L. rhachirhinchus		*Clarotes* sp.
	Lates cf. *L. rhachirhinchus*		*Lates* sp.
Lake Edward and Upper Semliki			? *Hyperopisus* sp.
			? *Synodontis* sp.
			Clarotes sp.
			Lates cf. *L. niloticus*
			? *Lates rhachirhinchus*

* The few Upper Pleistocene specimens from the Lake Edward – Upper Semliki area yielded *Lates* cf. *L. niloticus* and a cichlid, probably *Sarotherodon* sp.

cyprinid in the Edward–Albert Rift is from Middle Pleistocene deposits at Katanda (Greenwood 1959).

Too great an emphasis should not be placed on these 'absentees' since their apparent absence could well be an accident of preservation and collection, and not due to biological or distributional factors. Nevertheless, we are impressed by the paucity of Clariidae because these fishes are abundant in mid-Pleistocene deposits in this area, and even in Pliocene deposits of Egypt (Greenwood 1959, 1972). Clariid remains are common in the Miocene Bled ed Douarah formation of Tunisia but nothing definitely clariid was found in the Miocene beds of Sinda-Mohari, and possible early Pleistocene records for this area are of only a few bones whose identity, even familial, is doubtful (see above, p. 112). As no clariid remains were recovered from the Miocene beds of Rusinga Island (Kenya waters of Lake Victoria), the earliest positive East African record for the family is, therefore, the Lower Pleistocene of Olduvai (Greenwood & Todd 1970).

This absence of clariids from East African Tertiary and some earlier Quaternary deposits, contrasted with the abundance of clariid material from later deposits here and earlier ones in north Africa, and taken together with the known ecological tolerance of extant species, may perhaps suggest that clariids had not reached the lower latitudes by that time (see also Greenwood 1973b).

Basically the same arguments could be applied to the Cyprinidae (Greenwood 1972, 1973b) although these fishes show less ecological tolerance than the Clariidae, and their later fossil record is less complete.

Unfortunately we cannot be certain about the specific identity of the *Lates* remains from the Lower Miocene of Sinda-Mohari (p. 107), but there are indications that the bones were derived from *L. rhachirhinchus*, the endemic and specialized species so characteristic of earlier Pleistocene beds in this area (see above, p. 109).

Lower Miocene collections from the Lake Albert area (pp. 115–116 and Table I) are generically more depauperate than those from Sinda-Mohari, although *Sindacharax* is present and there is a strong suggestion of *L. rhachirhinchus* also being present. No Miocene material was obtained from the Lake Edward and Upper Semliki region of the rift.

The Pliocene or earlier Pleistocene fishes of Sinda-Mohari are essentially like those of the Lower Miocene. *Lates rhachirhinchus* is definitely present, possibly as the only species although not all the *Lates* material can be identified to species. The bagrid catfish *Auchenoglanis* is represented in the early Pleistocene collections, and there are fragments which may be attributable to a clariid catfish (p. 108).

Lates rhachirhinchus persisted in the Sinda-Mohari area until a little later in the Pleistocene (Villafranchian), and may also have done so in the Upper Semliki region (p. 118). In both places at that time, however, there was another *Lates* species which cannot be separated, on osteological features, from the extant *L. niloticus* (see above, pp. 118–119, also Greenwood 1959). *Lates* remains from the Villafranchian sites of Lake Albert (p. 117) cannot be specifically identified. Later material (Upper Pleistocene to Holocene) from the Upper Semliki–Lake Edward region is certainly not attributable to *L. rhachirhinchus*, and the species it represents would seem to be of *L. niloticus* type. In other words, the temporal range of the morphologically specialized *L. rhachirhinchus* was, at most, from Lower Miocene to Lower Pleistocene times. Its geographical range would seem to have been restricted to the Semliki valley.

The relationships of *L. rhachirhinchus*, especially its apparent affinities with the present-day *Lates* species flock of Lake Tanganyika, are discussed on p. 97. For the moment no definite conclusions can be drawn as to its phylogeny, but it is clearly as derivative a species as is either *L. mariae* or *L. microlepis* of Lake Tanganyika, and certainly more so than *L. angustifrons* of that lake.

Until the discovery of *Sindacharax lepersonnei*, the earliest record for characoid fishes in Africa was from the Pliocene of Wadi Natrun (*Hydrocynus* sp. and *Sindacharax deserti*). It is interesting to note that these early records are all of species with a highly specialized dentition, one species (*Hydrocynus*) being undoubtedly a piscivorous predator, the other two probably specialized herbivores.

Taken in its entirety, the new material from the Lake Edward–Albert Rift throws no further light on ecological conditions obtaining during the Miocene and Lower Pleistocene, nor on the history of the fauna (Greenwood 1959). The presence of a specialized and apparently endemic *Lates* species, however, may indicate some fairly lengthy period of isolation although alternative explanations are possible (see p. 98 above).

The Miocene fauna (Table I) suggests that ecological conditions at that time were probably little different from those in succeeding periods. In no period can the known fish fauna be used to decide whether the environment was that of a lake or a river. The presence of *Lates* may be taken to exclude the possibility of widespread swamp conditions because extant members of this genus are all restricted to well-oxygenated water.

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LOWER CRETACEOUS AMMONITES FROM NORTH-EAST ENGLAND: THE HAUTERIVIAN HETEROMORPH *AEGOCRIOCERAS*

P. F. RAWSON

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LOWER CRETACEOUS AMMONITES FROM NORTH-EAST ENGLAND: THE HAUTERIVIAN HETEROMORPH *AEGOCRIOCERAS*

BY

PETER FRANKLIN RAWSON

Department of Geology, Queen Mary College, University of London

Pp 129–159; 6 *Plates*; 3 *Text-figures*

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LOWER CRETACEOUS AMMONITES FROM NORTH-EAST ENGLAND: THE HAUTERIVIAN HETEROMORPH *AEGOCRIOCERAS*

By P. F. RAWSON

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ABSTRACT

Aegocrioceras is a common heteromorph ammonite in the Speeton Clay of Filey Bay, Yorkshire, where seven species occur, of which *A. compressum* and *A. spathi* are described herein as new. Another two species are provisionally included in the genus. A neotype of *A. raricostatum* (Phillips 1829) and a lectotype of *A. torulosum* (Koenen 1902) are designated. The stratigraphical horizons of most species have now been established : six are limited to parts of Bed C7, in which three discrete assemblage occur in a thickness of only 2·6 m of clay. The faunal and sedimentary sequence is condensed and probably incomplete. *A.* ? *seeleyi* occurs higher in the succession, in Bed C4L, and *A.* ? *koeneni* is probably from the same horizon.

The type species of *Aegocrioceras*, *A. capricornu* (Roemer), is not known from Speeton, but some north German examples are discussed. There are great similarities between the faunas of the two areas although the stratigraphy of the German faunas is still poorly known.

I. INTRODUCTION

Aegocrioceras is a distinctive capricorn heteromorph ammonite of mid-Hauterivian age, which is apparently endemic to north-west Europe. Although it is represented by abundant and varied forms, the sequence of species has never been established and the taxonomy is confused ; the confusion is emphasized by Spath's (1924) list (see p. 155) of the Speeton fauna in which over 20 taxa are recorded, many under unpublished names or as the misidentifications of earlier authors.

The sequence of species in the Speeton Clay, and the variation they exhibit, has been assessed as a result of the bed-by-bed collection of over 150 specimens. This collection has been divided between the British Museum (Natural History) and the University of Hull. Existing museum and private collections have also been studied and the more important specimens are referred to here. The research forms part of a study commenced during the tenure of a N.E.R.C. research studentship at the University of Hull and continued at Queen Mary College, partly during the tenure of a N.E.R.C. post-doctoral fellowship. Study of comparable faunas in Germany was assisted by awards from the Daniel Pidgeon Fund of the Geological Society of London (1969), the Central Research Fund of the University of London (1971) and the European Exchange Programme between the Royal Society and the Deutsche Forschungs-Gemeinschaft (1973).

I thank Dr E. Kemper and Dr Fr. Schmid (Hanover), Dr C. Spaeth (Hamburg), and the numerous colleagues mentioned in the first paper of this series (Rawson 1971a) for their considerable assistance, and Dr F. A. Middlemiss (Queen Mary College) for reading the manuscript.

II. PREVIOUS WORK ON THE SPEETON *AEGOCRIOCERAS*

Even as early as 1868, so much confusion was caused by the use of ill-defined names that Judd (1868 : 247–248), discussing the Speeton '*Ancyloceras*' (*Aegocrioceras*, *Crioceratites* and allies), warned 'in the large majority of instances, we find at Speeton small and detached fragments of a single whorl only, which for the purposes of identification and description are absolutely worthless, and which, if so made use of, can only be sources of error. For these reasons I think that the various species of this group, founded by Young and Bird, Phillips and Römer, generally on the smallest fragments, might with no loss, but much positive advantage, to palaeontology be suppressed.'

Of the authors that Judd referred to, Young & Bird (1828) only described one species of *Aegocrioceras*, *A. bicarinatum*, which has now been stabilized by the selection of a neotype (Howarth 1962). The specific names used by John Phillips are less problematic than subsequent usage (e.g. Koenen 1902 ; Spath 1924) has implied, for Phillips (1829) clearly referred most of his figured specimens to species already described by the Sowerbys. Though he eventually (Phillips 1875) expressed doubt on the identification of the Speeton forms with the Sowerby species, the specific names cannot be attributed to Phillips. Only one genuinely new name, *Hamites raricostatus*, can be referred to *Aegocrioceras* : a neotype for this species is now designated (see p. 143). Roemer (1841) described several new '*Hamites*', of which three, *Hamites subnodosus*, *H. semicinctus* and *H. capricornu*, belong to *Aegocrioceras*. The types are lost, but *A. semicinctum*, based partly on a Speeton specimen, is readily identifiable from Roemer's description and figure. *A. capricornu*, though frequently recorded and utilized as a zonal index in north Germany, is much more difficult to interpret and German stratigraphers have used it as a 'sack' name for any of the more compressed *Aegocrioceras*.

Buckland (1836) published a manuscript name of Phillips, *A. bucklandi*, which was used by most early collectors. A very active amateur at that time was William Bean (1787–1866), who originated several manuscript names (Rawson 1970 : 590) which enjoyed a wide circulation among contemporary collectors. The names are still visible on labels (sometimes in Bean's handwriting) in his own and other (e.g. Bowerbank's, Lady Hastings') collections : all were recorded in Spath's (1924) faunal list. One Bean manuscript name, *A. quadratum*, was eventually published by Crick (1898) and the lectotype of this species has now been described and refigured (Rawson 1970 : 585).

Despite the number of published and Bean manuscript names already familiar to the early and mid-nineteenth-century collectors, very few were listed in the essentially stratigraphical works of Leckenby (1859), Judd (1868) and Lamplugh (1889). All three authors referred to the occurrence of various '*Hamites*' or '*Crioceras*' and recognized two distinct horizons (Beds C7F and C7A of the modern nomenclature) characterized by large heteromorphs now assigned to *Aegocrioceras* and *Crioceratites*. Both Judd (1868) and Lamplugh (1889) stressed the difficulty of identifying the heteromorphs, and Judd's opinion has already been quoted.

Pavlow (1892) figured one of Lamplugh's specimens and noted that the fragments of '*Crioceras*' which he had examined suggested rather a diverse fauna. However, Danford's (1906) subsequent review of the Speeton ammonites shed little new light on this, for it included only a brief note on the heteromorphs. The three listed species referable to *Aegocrioceras* were identified by Dr A. von Koenen, who had earlier (Koenen 1902) made brief note of some Speeton forms. Spath's (1924) list of Speeton *Aegocrioceras* is essentially a compilation of records from existing collections and does not represent a critical revision of the fauna. The interpretation of some of the listed forms has recently been discussed (Rawson 1970) and is further elaborated upon in the appendix (p. 154).

Despite these numerous references to the Speeton *Aegocrioceras*, Pavlow's (1892) suggestion that the fauna would merit a more detailed palaeontological study has gone unheeded. A similar situation prevails in north Germany, where Roemer's (1841), Neumayr & Uhlig's (1881) and especially Koenen's (1902) monographs drew attention to the rich faunas of the 'capricornu-Schichten', yet stratigraphers have continued to 'lump' the various forms into three broad 'species', *A. semicinctum* (Roemer), *A. torulosum* (Koenen) [= *A. quadratum* (Crick)] and *A. capricornu* (Roemer).

III. LITHOSTRATIGRAPHY

Lamplugh's (1889) main subdivisions of the Speeton Clay and Fletcher's (1969) lithostratigraphical subdivision of the C Beds have been discussed in detail in an earlier paper (Rawson 1971a). With the exception of two species only questionably included in *Aegocrioceras*, the genus is apparently limited to Beds C7G to C7A, occurring through a vertical thickness of only 2·6 m of clay. No *Aegocrioceras* are known from the overlying Beds C6 and C5, but *A.* ? *seeleyi* (Neumayr & Uhlig) appears in Bed C4L and *A.* ? *koeneni* Spath is probably from this horizon.

The lithological subdivision of Bed C7 is as follows :

Bed		Thickness (*metres*)
C7A	Brown-weathering, silty, indurated clays with large calcareous lenticles, often partially phosphatized. *Crioceratites* spp., *Aegocrioceras spathi* sp. nov.	0·30
C7B	Pale grey clay. *A. spathi* sp. nov.	0·30
C7C	Dark grey clay with large pale mottles (*Chondrites*) at top	0·38
C7D	Pale grey clay with a little glauconite. *A. raricostatum* (Phillips), *A. compressum* sp. nov.	0·30
C7E	Black clay ; large, pale grey mottles (*Chondrites*) at top. Glauconite abundant at top, diminishing downwards. *A. compressum* sp. nov.	0·38
C7F	Pale grey clay with abundant flattened *Simbirskites* (*Speetoniceras*) sp.	0·15
	Pale grey, silty clay, weathering brown and locally indurated. Contains round, phosphatized nodules (up to 150 mm diameter) often enclosed in larger, more irregular calcareous concretions. Body chambers of *Aegocrioceras* are common, especially in the calcareous concretions. *A. quadratum* (Crick), *A. semicinctum* (Roemer), *A. bicarinatum* (Young & Bird), *Simbirskites* (*Speetoniceras*) sp.	0·23
C7G	Pale grey clay with *Chondrites*. *A. quadratum* (Crick), *A. semicinctum* (Roemer), *A. bicarinatum* (Young & Bird), *S.* (*Sp.*) *inversum* (M. Pavlow)	0·53
C7H	Dark grey clay with abundant glauconite. *S.* (*Sp.*) *inversum* (M. Pavlow), *S.* (*Sp.*) cf. *versicolor* (Trautschold)	0·30

These subdivisions are summarized in Text-fig. 2 (p. 151).

IV. SYSTEMATIC DESCRIPTIONS

Morphological terms used in the systematic descriptions are defined in the ammonoid volume of the *Treatise on Invertebrate Paleontology* (Arkell *et al.* 1957 : L2–L6).

Because of the fragmentary nature of most specimens, few parameters can be measured for statistical purposes. However, the ratio of whorl thickness to whorl height (*wt*/*wh*) can be obtained even for small fragments and expresses the relative compression of the whorl section (Table 1). For specimens above an estimated diameter of 10 mm the ratio shows no significant change during growth.

TABLE 1

Ratio of whorl thickness (*wt*) to whorl height (*wh*), for seven species of *Aegocrioceras*

Species	Number of specimens measured	Mean *wt*/*wh*
semicinctum	14	0·96
quadratum	46	0·92
bicarinatum	42	0·91
spathi	7	0·78
raricostatum	15	0·74
densiradiatum	3	0·71
compressum	7	0·67

The nature of the information included in certain sections of each specific description is outlined here.

Synonymy

With few exceptions, only papers in which specimens are illustrated are referred to in the synonymy. Reference is not normally made to Spath's (1924) faunal list, for although this has hitherto been the standard reference for the Speeton sequence there are considerable problems in interpreting the identifications in the absence of figures or descriptions ; a partial reinterpretation of Spath's records is included as an appendix to this paper (p. 154).

Certain symbols have been used to provide a more critical synonymy, as follows :

v (vidimus)	specimen seen by the author
v*	type specimen seen
d (deletum)	specimen is lost
d*	type specimen is lost

Material

The majority of the described specimens were collected by the author and are now in the British Museum (Natural History) (BM.) and the University of Hull (HU.Rn.). Additional specimens in other collections have been utilized where necessary, though the exact horizons of most are not recorded. These are from the following collections : British Museum (Natural History) (BM.), Hull Museum (HM.), the Museum of the Institute of Geological Sciences (GSM.) ; the Geologisches-Paläontologisches Institut, Göttingen (GPiG.) ; the Niedersächsisches Landesamt für Bodenforschung, Hanover (NLfB.) ; the Sedgwick Museum, Cambridge (SM.) ; the Yorkshire Museum, York (YM.) ; the University of Hull (HU.) ; and the private collection of Messrs C. W. and E. V. Wright (Wrights' collection).

The descriptions are based on 221 Speeton specimens, together with 12 north German specimens used for comparison. The 233 specimens are distributed among 10 species, as shown in Table 2.

TABLE 2

Distribution of the specimens studied among ten species of *Aegocrioceras*

Species	Number of specimens (including type)	
	Speeton	North Germany
A. bicarinatum (Young & Bird)	39	–
A. quadratum (Crick)	70	1
A. semicinctum (Roemer)	22	–
A. varicostatum (Phillips)	45	3
A. compressum sp. nov.	4	2
A. spathi sp. nov.	17	3
A. densiradiatum Rawson	8	–
A. capricornu (Roemer)	–	3
A. ? seeleyi (Neumayr & Uhlig)	5	–
A. ? koeneni Spath	11	–
	221	12

Dimensions of figured specimens

Where possible, the dimensions of figured specimens are given. Because the specimens are uncoiled, the distance between the dorsum of the last whorl and the venter of the preceding whorl is included in addition to the standard measurements. Dimensions (in millimetres) are therefore listed as follows – diameter : whorl height, whorl thickness, width of umbilicus, distance between dorsum and venter. These are followed by the number of ribs on the last whorl ; (e) = estimated dimension or rib number.

Suborder ANCYLOCERATINA Wiedmann 1966

Superfamily **ANCYLOCERATACEAE** Meek 1876

Family **ANCYLOCERATIDAE** Meek 1876

Subfamily **CRIOCERATITINAE** Wright 1952

The Crioceratitinae include a series of crioceratitid and small ancyloceratid heteromorphs of late Valanginian to Barremian age, together with normally coiled derivatives such as *Pseudothurmannia* and *Hemihoplites*. The heteromorph and normally coiled genera are linked by morphological transitions (Wiedmann 1962, 1969) and possess similar sutures with quadrilobate primary suture and characteristic I–U–L–E lobe formula throughout growth (Wiedmann 1969).

There are two main schools of thought concerning the origin of the Crioceratitinae. The sculptural resemblance and stratigraphical relationship between early Crioceratitinae and some of the immediately preceding, evolute *Acanthodiscus* and partly uncoiled *Distoloceras* led many of the earlier workers (e.g. Neumayr & Uhlig 1881 ; Kilian 1910) to derive the majority of the Crioceratitinae from the Neocomitinae ; this view was upheld by Sarkar (1955). On the other hand, sutural characteristics and the uncoiled shell of the Crioceratitinae suggest a close relationship with earlier heteromorphs and with the lytoceratid ammonites (Wright 1957 ; Thomel 1964). Wright (1957), Thieuloy (1965) and Wiedmann (1969) derived the Crioceratitinae monophyletically from the Protancyloceratinae. Wiedmann (1969) has put forward strong arguments for a monophyletic origin of all the 'Cretaceous' heteromorphs, placing them in the Suborder Ancyloceratina Wiedmann 1966. The earliest (Middle Tithonian) representatives are probably derived from a lytoceratid, though intermediate forms are not known (Wiedmann 1973 : 313).

The earliest Crioceratitinae appear to be the north German genus *Juddiceras* Spath and the southern French *Himantoceras* Thieuloy, both of Upper Valanginian age. I regard *Juddiceras* as a primitive crioceratitid rather than a late protancyloceratid because of its similarity to *Himantoceras acuticostatum* Thieuloy. *Himantoceras* was originally dated as basal Hauterivian (Thieuloy 1965) but has subsequently been assigned to the Upper Valanginian (Moullade & Thieuloy 1967 ; Thieuloy 1973).

Genus ***AEGOCRIOCERAS*** Spath 1924

TYPE SPECIES. *Hamites capricornu* Roemer 1841, by original designation.

Diagnosis. A genus with crioceratitid coiling and strong, single, radial ribs. Tubercles, mainly ventro-lateral, are common in juveniles but disappear with growth.

Description. The maximum diameter is at least 500 mm, the body chamber occupying $\frac{1}{2}$ to $\frac{2}{3}$ of a whorl. Coiling is crioceratitid throughout; adjacent whorls may be almost in contact or well separated. The whorl section is rounded to subquadrate, inflated to compressed, the dorsum varying from slightly impressed to slightly convex. Ornament consists of strong, single, rectiradiate, prorsiradiate or rursiradiate, straight or curved ribs which extend across the venter without interruption but are usually represented on the dorsum by forwardly curving, feeble rib-folds. The dorsum is also crossed by well-defined growth striae, which are less clearly visible on flanks and venter. On the early whorls small ventro-lateral tubercles are generally present on most ribs; these disappear with growth. In one species (*A. semicinctum*), mid-lateral and sometimes dorso-lateral as well as ventro-lateral tubercles occur on occasional ribs in early growth stages.

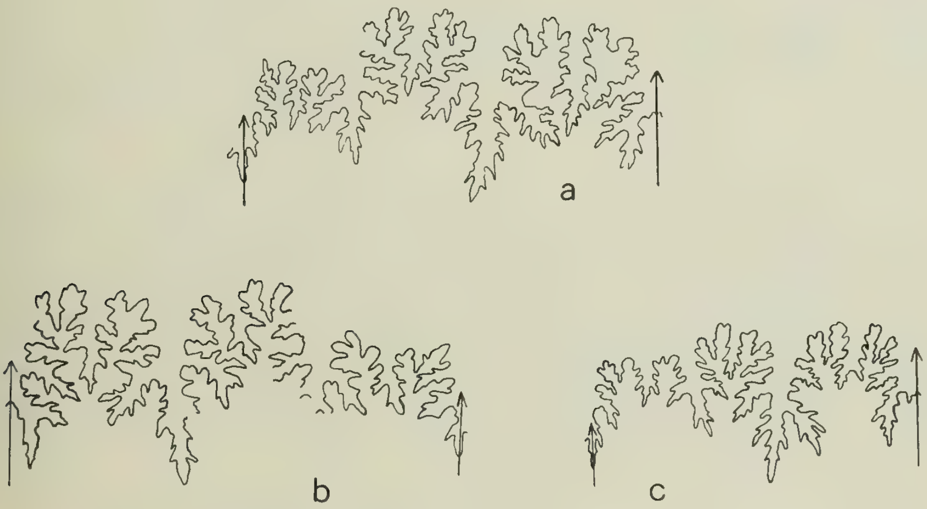

Fig. 1. Suture lines of *Aegocrioceras*. a, *A. bicarinatum* (BM. C78926). *b*, *A. quadratum* (BM. C79042). c, *A. raricostatum* (HU.Rn. 874).

The primary and first few subsequent sutures are not known, but the juvenile to adult growth stages have a quadrilobate suture. Each saddle is usually fairly deeply subdivided by a single, long lobelet, and adjacent sutures are normally in contact at their extremities, except in *A. raricostatum*.

Discussion. Spath (1924 : 76) introduced the generic name for a distinctive group of north-west European capricorn crioceratitids 'differing from *Crioceras* s.s. (*duvali* group) in ornament and suture-line'. The latter part of his statement cannot be supported, but the strong, relatively uniform simple ribs clearly differentiate *Aegocrioceras* from *Crioceratites* with its periodic stronger, bi- or tri-tuberculate ribs.

The origin of *Aegocrioceras* is problematic. In north-west Europe, no Crioceratitinae are known from the Lower Hauterivian *Endemoceras* beds, but *Aegocrioceras* appears suddenly, and in abundance, just above. Although this suggests an immigration from elsewhere there are no obvious immediate ancestors in France, where the Lower Hauterivian *loryi* group are typical *Crioceratites* (Thieuloy 1972 : pl. 5), or in any other known Lower Hauterivian faunas. It is possible that, despite the time gap, *Aegocrioceras* is a derivative of the Upper Valanginian *Juddiceras*, which occurs in north Germany.

The Tethyan genera *Leptoceras* Uhlig, of Berriasian and Valanginian age, and the homeomorphic *Leptoceratoides* Thieuloy from the Barremian are similar in general morphology to *Aegocrioceras*, but both are microconch genera growing to only about 30 mm diameter. The early identification of some Speeton *Aegocrioceras* with the French '*Crioceras*' *puzosianum* d'Orb. (e.g. Judd 1868) indicates at least a superficial similarity with another Tethyan form, though the latter is so poorly known that the true relationship remains obscure. Sarkar (1955 : 160) questionably included d'Orbigny's species in his new genus *Spathicrioceras*, but was unable to locate the type or any other example. He considered the age to be Barremian, 'after Kilian'. Uhlig (1883) thought the species was like a '*Leptoceras*', but d'Orbigny's figure could equally well be interpreted as an *Aegocrioceras* : in the absence of further material it is impossible to decide whether '*C.*' *puzosianum* is a *Spathicrioceras*, *Leptoceras*, *Leptoceratoides* or *Aegocrioceras*.

As 'genotype' of *Aegocrioceras*, Spath (1924 : 76) proposed ' "*Crioceras*" *capricornu* (Roemer) Pavlow (1892)'. This creates an immediate problem as Pavlow's (1892 : 154, pl. 18, fig. 9) '*capricornu*' belongs to *A. bicarinatum* (Young & Bird). It seems from the complicated taxonomic procedure followed throughout his paper that Spath regarded Roemer's (1841) and Pavlow's (1892) '*capricornu*' as the same species, and this is also apparent from some of the extant specimens bearing Spath's identifications. He apparently referred to Pavlow's figure rather than Roemer's because Pavlow's was much the better. Therefore according to I.C.Z.N. rules, *A. capricornu* Roemer, not *A. bicarinatum* (Young & Bird) (= '*capricornu*' Pavlow 1892), must be taken as the type species.

Aegocrioceras bicarinatum (Young & Bird)

Fig. 1a ; Pl. 1, fig. 2 ; Pl. 2, fig. 1

d* 1828 *Hamites bicarinatus* Young & Bird : 278, pl. 15, fig. 10.
v ? 1829 *Hamites alternatus* Sowerby ; Phillips : 123, pl. 1, fig. 27 (*non* fig. 26). (2nd edit. 1835 ; 3rd edit. 1875).
d 1892 *Crioceras capricornu* (Roemer) ; Pavlow : 154, pl. 19, fig. 9.
d 1902 *Crioceras capricornu* (Pavlow *non* Roemer) ; Koenen : 320.
v 1906 *Crioceras matheroni* d'Orbigny ; Koenen *in* Danford : 113.
v 1924 *Aegocrioceras subseeleyi* Spath : 77.
v 1962 *Aegocrioceras bicarinatum* (Young & Bird) Howarth : 209, pl. 19, fig. 8.
v 1969 *Aegocrioceras bicarinatum* (Young & Bird) ; Hiltermann & Kemper : 23, pl. 2, figs 1, 2.
v 1970 *Aegocrioceras subseeleyi* Spath ; Rawson : 587, figs 3–5.

TYPE. BM. 89107 (Bean collection), from the Speeton Clay of Speeton, was designated neotype and figured by Howarth (1962).

MATERIAL. 38 specimens (author's collection) from Speeton, mainly whorl fragments: 35 from Bed C7G (BM. C78926–78949; HU.Rn. 702–704, 933, 1031, 1065, 1100, 1106, 1166, 1200, 1211) and 3 from Bed C7F (HU.Rn. 367, 585, 935). There are about 20 specimens in the museum collections.

DESCRIPTION. The whorl is higher than wide ($wt/wh = 0{\cdot}91$), with a subquadrate whorl section. The flanks are gently rounded, angular at the ventro-lateral edge and rounded in the dorso-lateral region; the dorsum is flat or gently rounded. The whorl height increases fairly slowly. The ribs are single, sharp, rectiradiate or prorsiradiate and extend straight across the venter. Above about 35 mm diameter the ribs bend forward more strongly about two-thirds of the way over the whorl flank (Pl. 1, fig. 2). In the earlier growth-stages they bear feeble tubercles on the ventro-lateral edge; at first these are developed on every second or third rib, but above about 10 mm diameter they occur on every rib. They diminish and eventually disappear above about 35–40 mm diameter. The number of ribs per whorl increases gradually with growth; at diameters of 30–40 mm the estimated number varies between 35 and 45, while in the specimen of 48 mm diameter figured on Pl. 1, fig. 2, there are 43 ribs on the last whorl.

DIMENSIONS of figured specimens:

BM. C78933 (Pl. 1, fig. 2) 52·1. At 48·0: 15·8, 14·2, 23·5, 3·4. 43 ribs.
GSM. 17540 (Pl. 2, fig. 1) 27·4: 9·6, 7·5, 13·0, –. 35 ribs.

DISCUSSION. Young & Bird's (1828) original description is adequate though their figure is poor; the specific name was not used by subsequent authors (or by the early collectors) with the exception of Spath (1924: 78), who thought that it referred to a *Paracrioceras* from the B Beds. Howarth (1962: 209) reinterpreted *Hamites bicarinatus* as a species of *Aegocrioceras* and proposed a neotype. Spath's (1924: 77) record of '*A. intermedium* (Bean MS *non* Phillips)' probably refers to this specimen. Other examples of the species in old collections are variously labelled '*puzosianus*', '*bucklandi*', '*capricornu*', etc. The specific name '*bicarinatus*' alludes to the small ventro-lateral tubercles.

A. bicarinatum is the commonest species of *Aegocrioceras* in Bed C7G, and occurs also in the overlying Bed C7F. Usually only pyritized, septate inner whorl fragments are preserved, and the largest known specimen is an incomplete body chamber of an individual of about 100 mm estimated diameter. There is some variation in rib density, height of whorl, width of venter between the tubercles, strength of the tubercles and disposition of ribs; the neotype is towards one extreme, especially in possessing rectiradiate rather than prorsiradiate ribs. All variants differ from comparable growth stages of *A. semicinctum* in having a subquadrate instead of a rounded whorl section, and in lacking the mid-lateral tubercles distinctive of juvenile whorls of the latter species.

The inner whorls of *A. quadratum* are almost identical with *A. bicarinatum* in ratio of whorl thickness to whorl height, but these characters increase more rapidly in *A. quadratum*, the whorls remain almost in contact (compare Pl. 1, figs 1, 2) and the ventro-lateral tubercles disappear at a relatively early growth-stage, so that the ventro-lateral region appears gently rounded rather than angular. In addition, the ribs of *A. quadratum* become gently flexuous during growth, while those of *A. bicarinatum* merely develop a forward bend high on the flank (cf. Pl. 1, figs 1, 2).

Pavlow's (1892) figured specimen of '*Crioceras*' *capricornu*, refigured by Wright (1957 : L209 ; fig. 237, 3a, b) as *A. capricornu* (Roemer), belonged to *A. bicarinatum* : the specimen (formerly in the British Museum (Natural History) but now decomposed) was referred to by Koenen (1902 : 320) who noted that it differed from the true *A. capricornu* in its more rounded cross-section, denser ribbing and more rapid increase in whorl thickness.

A. subseeleyi Spath is regarded as a junior subjective synonym of *A. bicarinatum*. The lectotype of Spath's species (Rawson 1970 : 587) is refigured here (Pl. 2, fig. 1) ; it was identified by Dr A. von Koenen as '*Crioceras matheroni*' and so recorded by Danford (1906 : 113). It differs from typical *A. bicarinatum* in having strongly prorsiradiate, more widely spaced ribs and a more compressed whorl, but extreme variants of *A. bicarinatum* show one or another of these features. One of the original syntypes of *A. subseeleyi*, the specimen figured by Phillips (1829 : pl. 1, fig. 21) as '*Ancyloceras alternatus* Sowerby', can only questionably be attached to *A. bicarinatum* because of its small size.

DISTRIBUTION. Speeton, Heligoland, north Germany.

Aegocrioceras quadratum (Crick)

Pl. 1, figs 1, 3, 4 ; Pl. 2, fig. 2 ; Pl. 3, fig. 1 ; Text-fig. 1

v*	1898	*Crioceras quadratum* (Bean MS) Crick : 74, 79, pl. 17, figs 10–13.
v	1902	*Crioceras torulosum* Koenen : 320, pl. 15, figs 4, 5.
v*	1968	*Aegocrioceras quadratum* (Crick) Jordan : 50.
v*	1970	*Aegocrioceras quadratum* (Crick) ; Rawson : 585, figs 1, 2.

TYPE. BM. 89102 (Bean collection), from the Speeton Clay of Speeton, was designated lectotype and figured by Rawson (1970).

MATERIAL. 69 specimens (author's collection) from Speeton, mainly body chamber fragments : 1 almost complete specimen (BM. C78996), 59 body chambers (BM. C78997–79033 ; HU.Rn. 356–360, 1243–1245, 1329–1336, 1407–1409, 1440–1442) and 1 septate inner whorl (BM. C79034) from Bed C7F ; 5 body chambers (BM. C79035–39) and 3 septate inner whorls (BM. C79040–42) from Bed C7G. 1 specimen from north Germany : GPiG. (uncatalogued).

DESCRIPTION. The whorl height increases moderately quickly so that the whorls remain almost in contact throughout growth. The whorl section is quadrate or subquadrate, the whorl flanks almost flat, either parallel or converging towards the venter. The venter is gently rounded, the dorsum flat or slightly concave (impressed), with slightly angular dorso-lateral region. The ribs are single, strong, initially straight and feebly prorsiradiate, becoming gently flexuous above about 40 mm diameter and remaining so to the adult body chamber. The ribs are usually rectiradiate in general course on these whorls. At first, the ribs bear small ventro-lateral tubercles, stronger ones alternating with weaker, but these soon disappear and above about 20 mm diameter the venter becomes gently rounded.

Dorsal muscle scars are visible on some specimens (BM. C79001, C79010, C79013 89102, C7154); they consist of two approximately semicircular smooth areas bounded by a shallow groove, and lie immediately anterior to the last septum.

DIMENSIONS of figured specimens:

BM. C79040 (Pl. 1, fig. 1). 57·8 : 21·3, 19·3(e), 26·0, 1·1(e). 41(e) ribs.
BM. C79041 (Pl. 1, fig. 3). 51·1 : 16·7, 16·5, 23·9, –.

DISCUSSION. The lectotype bears William Bean's original label '*Crioceratites quadratus*', a name finally published by Crick (1898). It consists of nearly half a whorl of body chamber with maximum whorl height 51·3 mm and thickness 43·4 mm. The ratio *wt/wh* is 0·85. Comparable body chambers, though normally with somewhat more inflated section (mean *wt/wh* = 0·92), are abundant in Bed C7F and reach a reasonably constant size (estimated diameters of 120–150 mm), which suggests that they are adult even though few show clearly adult features. This reflects the fact that the last few septa and the aperture are rarely preserved: occasionally the last few preserved ribs are closer together and less coarse.

The mean *wt/wh* is extremely close to that of the much smaller specimens of *A. bicarinatum* (0·91). However, the association of body chambers and inner whorls in 2 specimens of *A. quadratum* (e.g. Pl. 1, fig. 4) has allowed comparison with a few smaller, septate specimens (Pl. 1, figs 1, 3) which differ from *A. bicarinatum* in being more tightly coiled, with more flexuous ribs and less well-developed ventro-lateral tubercles. At all growth-stages, *A. semicinctum* has a more rounded whorl section than *A. quadratum*, and less numerous, slightly less flexuous ribs.

A. quadratum is quite common in north Germany, where it has usually been recorded as *A. torulosum* (Koenen). There is no significant difference between the syntypes of Koenen's species[1] and the lectotype of *A. quadratum*, so that *A. torulosum* is here regarded as a junior subjective synonym of *A. quadratum*.

DISTRIBUTION. Speeton, Heligoland, north Germany.

Aegocrioceras semicinctum (Roemer)

Pl. 2, fig. 3; Pl. 3, figs 2, 3

d ? 1829 *Hamites maximus* Sowerby; Phillips: pl. 1, fig. 20 (*non* fig. 21). (2nd edit. 1835, 3rd edit. 1875).
1841 *Hamites semicinctus* Roemer: 92, pl. 15, fig. 3.
v 1902 *Crioceras semicinctum* (Roemer) Koenen: 322, pl. 15, fig. 1.
v 1970 *Aegocrioceras semicinctum* (Roemer) Rawson: 591.
v 1970 *Aegocrioceras ligatum* (Bean MS); Rawson: 591.

TYPE. One syntype, the Speeton Clay specimen figured by Phillips (1829: pl. 1, fig. 20) as '*Hamites maximus* Sowerby', is lost; the Heligoland specimen figured by

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[1] The original of Koenen 1902: pl. 15, fig. 5 is here designated lectotype of *Aegocrioceras torulosum* (Koenen).

Roemer may still exist though it has not yet been traced. The species is interpretable from Roemer's description and figure, but will not be stabilized by designation of a lectotype or neotype until further enquiries have been made about the missing syntype.

MATERIAL. 21 specimens. In the author's collection 3 fairly complete specimens (BM. C78950–52) and 11 body chambers (BM. C78953–59; HU.Rn. 105, 676, 823, 1186) from Bed C7F; 2 inner whorl fragments (BM. C78960–61) from Bed C7G. In other collections 5 almost complete specimens in nodules of Bed C7F type: GSM. 17495, 22226 (Danford collection); SM. B53171; YM. 885, PR/1975/1 (Bean collection); Wrights' collection 21849.

DESCRIPTION. The shell is fairly tightly coiled, the whorl height increasing moderately rapidly; the whorl section is almost circular but slightly higher than wide ($wt/wh = 0{\cdot}96$). The dorsum is flat, the dorso-lateral edge and flanks rounded, the venter flat on inner whorls becoming more rounded with growth. The strong, single, radial ribs are initially straight and rectiradiate: later they become rursiradiate and may be slightly flexuous. The inner whorls bear small ventro-lateral tubercles on most ribs; these gradually diminish and eventually disappear at diameters of 40–50 mm. In the earliest whorls occasional tubercles are more strongly developed, and up to about 25–30 mm diameter mid-lateral and sometimes dorso-lateral tubercles occur on some ribs.

Muscle scar impressions are preserved on one specimen (HU. Rn.105); they are like those of *A. quadratum*.

DIMENSIONS of figured specimens:
GSM. 22226 (Pl. 2, fig. 3). 86·1: 30·3(e), 29·8, 42·4(e), 4·0(e). 46 ribs.
YM. 885 (Pl. 3, fig. 3). 75·3: 25·2, –, 34·2, 3·3. 41 ribs.

DISCUSSION. At Speeton, *A. semicinctum* is represented mainly by body chamber fragments, but several specimens have earlier whorls preserved. Although definite adult characters are difficult to distinguish, the relatively constant size of body chambers from the same nodule band (in C7F) that also yields consistently larger body chambers of *A. quadratum* suggests that *A. semicinctum* generally grew to a diameter of about 100–120 mm.

There is some variation in whorl proportions and degree of uncoiling, but none of the variants is as tightly coiled as *A. quadratum*. *A. semicinctum* differs from other species in its inflated, subcircular whorl section and in having mid-lateral tubercles in the inner whorls. Body chambers are distinguished from those of *A. quadratum* by their less flexuous, stronger, rursiradiate ribs and rounded instead of subquadrate whorl section, though a few specimens appear intermediate in form and are difficult to distinguish.

William Bean applied his manuscript name '*Crioceratites ligatus*' to *A. semicinctum*: in addition to the York Museum specimen (Pl. 3, fig. 3) previously recorded as bearing a Bean label (Rawson 1970: 591) there is another specimen at York. A third example (Bean collection, BM. 89101) is of an indeterminate species. Subsequent collectors applied the name indiscriminately.

DISTRIBUTION. Speeton, Heligoland, north Germany.

Aegocrioceras raricostatum (Phillips)

Fig. 1c. ; Pl. 4, figs 6–10 ; Pl. 5, figs 3, 4, 7

d* 1829 *Hamites raricostatus* Phillips : pl. 1, fig. 23 (2nd edit. 1835, 3rd edit. 1875).
d *non* 1841 *Hamites raricostatus* Phillips ; Roemer : 93, pl. 13, fig. 14.
d ? 1902 *Hamites raricostatus* Phillips ; Koenen : 320.
v 1902 *Hamites intermedius* Phillips (*non* Sowerby) ; Koenen : 319.
v 1906 *Hamites intermedius* Phillips ; Koenen *in* Danford : 114.
v 1924 *Aegocrioceras intermedium* (Phillips) Spath : 76, 77.
v 1924 *Toxoceratoides rotundus* Bean MS *non* Phillips ; Spath : 78.
v 1970 *Aegocrioceras* sp. nov. Rawson : 589.
v 1971b *Aegocrioceras* sp. nov. Rawson 1970 ; Rawson : 70.

Type. The holotype, originally in the Williamson collection in Scarborough Museum, is lost ; BM. C78963 (author's collection), from Bed C7D of the Speeton Clay, is here designated neotype.

Material. 44 specimens from Speeton and 3 from north Germany. Speeton : (author's collection) BM. C78964–72 from Bed C7D ; HU.Rn. 99, 874, 941, 942 (no horizon) ; (other collections) HU. Neale collection S943, S1526–28, S1530 ; HM. 22/64/12 ; BM. C72669, C78973, C72671 (Lamplugh collection), 89106 (Bean collection), C78962 (Kelly collection) ; GSM. 17449, 17480, 17482–7, 17489, 17490, 17492, 17502 (all Danford collection), 32137, 32140, 32151 (Marchioness of Hastings collection), 32135 ; SM. B53164 (Leckenby collection), 53148 ; Wrights' collection 10386, 20392. North Germany : NLfB. Kh.67 ; GPiG. (two uncatalogued specimens).

Description. The whorl height is low in relation to diameter and increases very slowly ; adjacent whorls are well separated. The whorl is moderately compressed ($wt/wh = 0{\cdot}74$) with flat or gently curved flanks and subrectangular to oval section ; the ventro-lateral and dorso-lateral edges are rounded and merge into the flanks except in specimens less than about 10 mm diameter where small ventro-lateral tubercles impart a slight angularity to this region. The dorsum varies from almost flat to convex. The ribs are strong, simple and widely spaced ; on the whorl flanks they are slightly prorsiradiate in general course but convex forwards, usually curving gently backwards near and over the venter. The dorsum bears well-developed, though small, forwardly curving rib-folds. The septa are well spaced, and individual lobes and saddles not very deeply subdivided (Fig. 1c), so that adjacent sutures are clearly separated from one another throughout their length.

Discussion. Phillips (1829, 1835, 1875) did not describe the species and his figure was sketchy ; as the holotype is lost both Howarth (1962 : 129) and the author (Rawson 1970 : 590) have regarded *A. raricostatum* as uninterpretable. However, among the numerous whorl fragments now attributed to this species several agree fairly closely with Phillips' figure in having widely spaced ribs, and the 2 specimens in the Wrights' collection (e.g. Pl. 5, fig. 3) are an almost perfect match. All exhibit the gentle shell curvature which is also indicated by Phillips' figure, and in some specimens the ribs also thicken towards the venter exactly as he indicated. The sparsely ribbed forms such as the holotype are clearly an extreme form of a variable assemblage whose more typical, relatively closely ribbed members include the specimens (e.g. GSM. 17484–7) which Koenen (1902), Danford (1906) and Spath (1924) recorded as *A. intermedium* 'Phillips' and Rawson (1970) described as *A.* sp. nov. The specimen now selected as neotype of *A. raricostatum* is intermediate between these and Phillips' holotype in rib density ; its maximum whorl height is about the same as the minimum height on Phillips' illustration.

In addition to this variation in rib density, there is some in whorl proportions. This is particularly apparent in the juvenile whorls, where forms with a more rounded whorl and relatively low height exemplify a very distinct variant. A small specimen in the Bean collection (BM. 89106 : Pl. 4, fig. 7) bears Bean's original label '*Hamites rotundus* Phillips', while a larger one in the Lamplugh collection (BM. C72671 : Pl. 4, fig. 10) bears a modern label '*Toxoceratoides rotundus* Bean MS non Phillips' which Mr D. Phillips informs me was probably copied from an earlier Spath label : these are presumably the originals of Spath's record of *T. rotundus* (Bean MS *non* Phillips) from the Upper B Beds. The Lamplugh specimen has an associated, but loose, label recording it from the B Beds. In fact, both specimens are extremely close to a fragment of intermediate size from Bed C7D (Pl. 4, fig. 9) which has a *wt/wh* ratio of 0·90, compared with a mean ratio 0·74 for the typical compressed forms of *A. raricostatum.*

Nearly all the specimens of *A. raricostatum* consist of short fragments, and specimens of more than half a whorl are rare at Speeton. The curvature of these bigger pieces is usually slightly irregular, but this is probably a result of post-depositional deformation, for regular curvature is apparent in some north German examples. The latter include fragments indicating that the species attained a diameter of at least 200 mm.

A. raricostatum is most closely approached in rib style and density by *A. spathi*, and both species were labelled '*raricostatum*' by the early collectors. However, *A. raricostatum* is distinguished from this and other *Aegocrioceras* by the loosely coiled, gently curved shell and very slow increase in whorl height. The septa are more widely spaced and the elements of the suture shorter and less deeply subdivided than in other species. The Heligoland specimen figured by Roemer (1841) as *Hamites raricostatus* apparently had ventro-lateral tubercles and does not therefore agree with the Speeton forms.

DISTRIBUTION. Speeton, Heligoland (Rawson 1974), north Germany.

Aegocrioceras compressum sp. nov.

Pl. 5, figs 2, 6

v 1971b *Aegocrioceras* sp. a Rawson : 70.

DIAGNOSIS. A very compressed species with feebly convex ribs which curve slightly backwards over the venter. Some ribs are intercalated low on the whorl flank and a few stand out more sharply than the rest.

HOLOTYPE. BM. C78974 (author's collection) from Bed C7D of the Speeton Clay, Speeton.

Paratypes. 5 whorl fragments, all collected by the author. BM. C78975–6 from Bed C7E, Speeton; BM. C78977 (no horizon), Speeton; NLfB. Kh.68, 69 from the *Aegocrioceras* Zone at Ovenstadt, near Petershagen, north Germany.

Description. The whorl height increases moderately quickly and the whorls are probably fairly tightly coiled. The shell is compressed (wt/wh = 0·67) with flat flanks, gently rounded venter and nearly flat dorsum. The ribs are single, almost straight at first but soon becoming slightly convex towards the aperture and curving gently backwards over the venter. Initially the ribs are of equal strength and bear feeble ventro-lateral tubercles; the tubercles disappear by about 10 mm diameter, while above about 20 mm diameter some ribs stand out slightly more sharply than the rest and a few of the intervening ribs are intercalated low on the whorl flanks instead of appearing at the umbilical edge. Most of those ribs which extend down to the umbilical edge form strong, forwardly curving folds on the dorsum.

Dimensions of figured specimen:
BM. C78974 (Pl. 5, fig. 2). 41·1: 13·4, 8·9, 19·4, –.

Discussion. The various whorl fragments assigned to this species, of which the holotype is the most complete, represent growth stages to an estimated diameter of 150 mm. All are distinguished from other *Aegocrioceras* by the occurrence of occasional slightly stronger ribs and the very compressed shell. *A. densiradiatum* approaches *A. compressum* in the compression of the shell (wt/wh = 0·71) and in the occurrence of occasional intercalated ribs, but has more numerous, finer ribs of approximately equal strength.

Distribution. Speeton, north Germany.

Aegocrioceras spathi sp. nov.

Pl. 4, figs 1, 2, 5

d ? 1881 *Crioceras* n. f. cf. *capricornu* Roemer; Neumayr & Uhlig: 67, pl. 53, fig. 5.
v 1971b *Aegocrioceras* sp. b Rawson: 70.

Diagnosis. A fairly compressed species (wt/wh = 0·78) in which the whorl height increases moderately quickly in relation to diameter. The ribs are convex forwards on the whorl flank and curve gently backwards over the venter.

Holotype. BM. C78978 (author's collection) from the Speeton Clay. The specimen was not found *in situ* but is in a red siltstone matrix which matches Bed C7A, from which 3 paratypes have been collected.

Paratypes. 19 specimens from Speeton and 3 from north Germany. Speeton: (author's collection) BM. C78979–84 from Bed C7B, C78985 from C7A; HU.Rn. 117, 633 from Bed C7A; HU.Rn. 399, 938 horizons not known. (Other collections) BM. 89100 (Bean collection); C72668 (Lamplugh collection); GSM. 17496 (Danford collection); Wrights' collection 6297–9; YM. PR/1975/2–3. North Germany: NLfB. Kh.66 (author's collection) from Sarstedt; GPiG. (two uncatalogued specimens) from Schulenburg.

Description. The whorl height increases moderately quickly though the whorls remain well separated. The shell is moderately compressed with subrectangular whorl section ($wt/wh = 0{\cdot}78$) ; the flanks are almost flat, the venter gently rounded and the dorsum flat. The ventro-lateral region is rounded except in the earliest growth stages (to about 10 mm diameter) where small tubercles occur. The ribs are single, strong, slightly convex towards the aperture on the flanks and curving gently backwards over the venter. They are rectiradiate or prorsiradiate in general course. In early growth stages the dorsum is crossed by feeble rib-folds and growth striae, which curve gently forwards ; on later whorls it is crossed by growth striae only. The number of ribs increases gradually with growth, from about 33 at 14 mm diameter (BM. C78980) to 35 at 45 mm (NLfB. Kh.66) and 44 at 67 mm diameter (BM. 89100).

Dimensions of figured specimen :
BM. C78978 (Holotype : Pl. 4, fig. 2). 52·3. At 47·9 : 14·5, 10·5, 25·0(e), –. Approx. 35 ribs.

The figured paratypes are slightly crushed or distorted.

Discussion. *A. spathi* shows slight variation in both the rapidity with which the whorl height increases and in degree of curvature of the ribs. Several specimens have at least one complete whorl preserved ; of these, the holotype, BM. C72668, BM. C89100 and YM. PR/1975/2 are preserved in a red siltstone matrix which matches the lithology of the prominent siltstone Bed C7A, from which 3 other specimens were collected. BM. C89100 was collected by William Bean and bears his original label '*Crioceratites raricostatus*'. It is the largest known Speeton specimen of *A. spathi* and has a diameter of about 93 mm, but fragments of much larger individuals of *A.* cf. *spathi* from north Germany (author's collection) indicate that the species probably grew to at least 300 mm diameter.

A. spathi is slightly more coarsely ribbed than *A. raricostatum*, the whorls are less well separated, the whorl height expands more rapidly and the dorsum is flatter. *A. capricornu* has relatively straight, sharper, more numerous ribs and the whorls are a little more inflated and much closer together than those of *A. spathi*. *A. compressum* is more compressed and has less regular, denser ribbing. The specimen from Egistorf figured by Neumayr & Uhlig (1881) is probably a variety of *A. spathi* with almost straight, slightly more closely spaced ribs.

Distribution. Speeton, Heligoland (Rawson 1974), north Germany.

Aegocrioceras densiradiatum Rawson

Pl. 6, fig. 2

v	1906	*Crioceras puzosianum* ? d'Orb ; Koenen *in* Danford : 113.
v	1924	*Aegocrioceras* sp. nov. aff. *capitanei* (Bean MS) ; Spath : 77.
v*	1970	*Aegocrioceras densiradiatum* Rawson : 589, figs 8–10.

Type. The holotype, BM. C72704 (Bean collection) from the Speeton Clay of Speeton, is refigured here (Pl. 6, fig. 2).

MATERIAL. In addition to the holotype and 4 paratypes (BM. C75710 ; GSM. 17498, 32125–6), there are 3 additional specimens from Speeton : BM. C78986–87 (author's collection), horizon not known ; GSM. 17479 (Danford collection).

DISCUSSION. The exact horizon of this species is still not known, but the Danford collection specimens are labelled 'Zone C' (GSM. 17498) and 'C6' (GSM. 17479). Specimens BM. C78986–87 (author's collection) were picked up on the lower part of the weathered slopes of Middle Cliff, where Beds C5–7 crop out. A middle C Beds horizon for this form would negate a tentative suggestion (Rawson 1970 : 589) that it may have given rise to *Hoplocrioceras phillipsi* (Phillips), since the latter probably occurs much higher, in the upper part of the Lower B Beds (Rawson 1975).

A. densiradiatum is distinguished from all other species of *Aegocrioceras* by its fine, dense ribs. In general whorl proportions it is most closely approached by *A. capricornu* and *A. compressum*, and, like the latter, *A. densiradiatum* has very occasional intercalated ribs. However, *A. compressum* has intermittent stronger ribs and a slightly more compressed whorl section.

DISTRIBUTION. Speeton.

Aegocrioceras capricornu (Roemer)

Pl. 5, fig. 1

d* 1841 *Hamites capricornu* Roemer : 92, pl. 14, fig. 6.

DISCUSSION. Although this is the most frequently quoted species in the German literature, it remains difficult to interpret. Roemer's (1841) figured 'syntype' (possibly two specimens) is lost ; it is this Heligoland specimen that was relied upon by subsequent German workers for the interpretation of the species. However, Roemer also referred Phillips' (1829 : pl. 1, fig. 22) figured '*Hamites intermedius*' to *A. capricornu*, and this is therefore another syntype. Phillips' specimen is also probably lost, for the partially decomposed specimen in the Yorkshire Museum (YM. 419A) labelled as his original does not match the figure at all closely. *A. capricornu* is best stabilized by selection of a neotype that will conform with German palaeontologists' usage. Neumayr & Uhlig (1881 : 194) probably interpreted the species correctly, though their figured specimens were all larger than Roemer's (1841) Heligoland original(s). Two fragmentary specimens (Neumayr & Uhlig 1881 : pl. 53, figs 6, 7) from the Schloenbach collection are in the Zentrales Geologisches Institut, Berlin, and have been loaned to me through Dr Vogel. One (fig. 6) is an internal mould, while the other has shell preserved and is a slightly less inflated form. The most complete individual (pl. 53, fig. 4), from the Strombeck collection, is lost.

A. capricornu is characterized by whorls which, though uncoiled, are almost in contact (Neumayr & Uhlig 1881 : pl. 53, fig. 4). The whorl is higher than wide, with subquadrate whorl section and flat flanks (Roemer 1841 : 92). The strong radial ribs are straight or feebly prorsiradiate, at least in the earlier whorls, being prominent and sharp where the shell is preserved but more rounded and distinctly broader and flatter over the venter in internal moulds. Whorl fragments with this style of ribbing are common in the German *Aegocrioceras* Zone, but more complete specimens are rarely found and are poorly represented in the museum collections. A specimen from Osterwald, near Hanover, figured here (Pl. 5, fig. 1) as *A. capricornu*, differs from Neumayr & Uhlig's figured specimens only in the change from straight, rectiradiate ribs in the inner whorls to slightly curved, rursiradiate ribs above about 60 mm diameter. This more advanced rib pattern approaches that of some much larger individuals from the *Aegocrioceras* Zone of Hildesheim which Koenen (1902 : pl. 16, figs 1–4) figured as *A. capricornu.*

None of the Speeton *Aegocrioceras* can be identified as *A. capricornu.* With the exception of *A. quadratum*, all have more widely separated whorls. The whorl height of *A. capricornu* increases less rapidly than that of *A. quadratum*, and in whorl proportions *A. capricornu* is between that species and the more compressed group of *A. spathi* and *A. raricostatum.* The ribs of the last two species are convex forwards on the flanks and curve gently backwards over the venter, where they remain narrow and sharp even on internal moulds. In general morphology *A. capricornu* therefore lies between the early *Aegocrioceras* of the *quadratum* group and the younger, more compressed forms ; it is provisionally inserted in this position in Fig. 3 (p. 151).

DISTRIBUTION. North Germany.

Aegocrioceras ? seeleyi (Neumayr & Uhlig)

Pl. 6, fig. 1

1881 *Crioceras seeleyi* Neumayr & Uhlig : 54, pls 51, 52.
1902 *Crioceras* cf. *seeleyi* Neumayr & Uhlig ; Koenen : 280.
1904 *Crioceras seeleyi* ? Neumayr & Uhlig ; Koenen : 42.

MATERIAL. 4 whorl fragments from Speeton, 1 from Flamborough. BM. C78988–89 (author's collection) from Bed C4L, Speeton ; HU. Neale collection S.705, S.1507 from Speeton ; BM. C78990 (collected by Mr M. Howgate) from the Speeton Clay erratic at Flamborough Head.

DISCUSSION. The German specimens figured by Neumayr & Uhlig (1881), though variable, all apparently belong to one species characterized by a subquadrate whorl section and slightly flexuous ribs of which occasional ones are slightly stronger and bear well-developed ventro-lateral tubercles, sometimes with feeble dorso-lateral and even mid-lateral tubercles : the Speeton fragments fit well within the range of variation of the north German examples that I have examined. Because of the slightly stronger ribs and the well-developed tubercles, both *A. seeleyi* and *A. koeneni* (described below) are difficult to assign to a genus. Although they stand apart from typical *Aegocrioceras* they also lack the periodic well-defined, strong, bi- or trituberculate ribs of *Crioceratites*. It is, therefore, hardly surprising that Spath (1924 : 84) regarded '*Crioceras*' *seeleyi* as a transitional link between *Aegocrioceras* and *Crioceratites*, while including both this species and *A.* ? *koeneni* in *Aegocrioceras*. However, there is a stratigraphical gap between the *Aegocrioceras* fauna of Bed C7 and *A.* ? *seeleyi*, typical *Crioceratites* occurring both with and between the two, so that the 'transitional' nature of *A.* ? *seeleyi* may be fortuitous. Its exact origin remains obscure, but it could be an offshoot from contemporaneous *Crioceratites* rather than from earlier *Aegocrioceras*.

The inner whorls of *A.* ? *seeleyi* have never been described, and I have failed to find associated outer and inner whorls either in the field or in German or English museums. Circumstantial evidence suggests that *A.* ? *koeneni* may represent these inner whorls : in addition to their morphological similarity, the two species occur together in north Germany, where I have collected them from a horizon in the *ihmensis* Subzone about 9 m above the *Aegocrioceras* Zone at Ziegelei Moorberg, Sarstedt. Mr M. Howgate has collected fragments of both species from the Speeton Clay erratic at Flamborough Head described by Kendall & Wroot (1924 : 788). At Speeton, *A.* ? *seeleyi* occurs in Bed C4L with the zonal fossil *Simbirskites* (*Craspedodiscus*) *gottschei* (Koenen) but the horizon of *A.* ? *koeneni* is not known.

Distribution. Speeton, Flamborough, Heligoland, north Germany.

Aegocrioceras ? koeneni Spath

Pl. 4, figs 3, 4 ; Pl. 5, fig. 5

d* 1829 *Hamites maximus* Sowerby ; Phillips : 123, pl. 1, fig. 21 (*non* fig. 20). (2nd edit. 1835).
d* 1875 *Ancyloceras grande* (Forbes) Judd ; Phillips : 274, pl. 1, fig. 21 (*non* fig. 20).
d* 1924 *Aegocrioceras koeneni* Spath : 77.
v 1969 *Aegocrioceras koeneni* Spath ; Hiltermann & Kemper : 23, pl. 2, fig. 7.
v 1970 *Aegocrioceras koeneni* Spath ; Rawson : 587, figs 6, 7.

Type. The neotype, HU. Neale collection S.1731, from the Speeton Clay of Speeton, was designated by Rawson (1970) and is refigured here, Pl. 4, fig. 3.

Material. 10 whorl fragments from Speeton (exact horizons not known) : BM. C78991–94 (author's collection), C72171 (W. T. Dean collection) ; HM. 22/64/13 ; HU. Neale collection S.576, S.1516, S.1521 ; Wrights' collection 19053. 1 small fragment from the Speeton Clay erratic, Flamborough Head, BM. C78995 (collected by Mr M. Howgate).

Description. The species is only known from septate whorl fragments of specimens up to about 50 mm diameter. The shell is moderately compressed with subquadrate whorl section and flat flanks. The dorsum is flat or slightly concave, crossed by forwardly curving rib-folds. The ribs are strong, simple, straight and rectiradiate or gently prorsiradiate on the lower part of the flank but curving forward more strongly nearer the venter. The ribs thicken towards and on the narrow venter, where some are raised slightly higher than the rest. Most ribs swell feebly at the ventro-lateral edge, which thus appears angular.

Discussion. The strong forward curvature of the ribs near the venter and the increase in height and thickness of some ribs in the ventral region distinguish *A.* ? *koeneni* from the comparable growth stages of all other *Aegocrioceras*. The largest specimen known (Pl. 4, fig. 4) is only about 50 mm in diameter, but more advanced growth stages of this species may be represented by *A.* ? *seeleyi*.

Distribution. Speeton, Flamborough, Heligoland, north Germany.

Other available specific names

Aegocrioceras bucklandi (Buckland). Buckland's (1836 : 65, pl. 44, fig. 1) figure indicates a rib curvature and degree of uncoiling reminiscent of *A. spathi* or *A. varicostatum* ; the holotype could, however, be the same specimen which Phillips (1829) had earlier figured as *Hamites intermedius* (Sowerby) (Rawson 1970 : 590) and which is also a syntype of *Hamites capricornu* Roemer 1841. Fragments of a partially decomposed specimen in the Yorkshire Museum (tablet 419A) are labelled as Phillips' original, though the attribution is doubtful (see also p. 147). This specimen is closest to some of the extremes of *A. bicarinatum*, to which species the name '*bucklandi*' was often applied by early collectors (e.g. Marchioness of Hastings collection). In view of all the problems of interpretation attached to Buckland's species, the name '*Hamites bucklandi*' should fall into disuse.

Aegocrioceras subnodosum (Roemer). Roemer's (1841 : 93, pl. 13, fig. 10) figured '*Hamites subnodosus*' is a short whorl fragment of an indeterminate *Aegocrioceras*. From his figure and brief description it could be an example of *A. bicarinatum* (Young & Bird 1828). Roemer's specific name has been little used by subsequent workers, though it was listed by Spath (1924).

V. THE SUCCESSION OF SPECIES IN THE SPEETON CLAY

Species subsequently assigned to *Aegocrioceras* have long been known to characterize a narrowly defined horizon (Bed C7) at Speeton (e.g. Leckenby 1859 ; Judd 1868 ; Lamplugh 1889), which Spath (1924) attempted to subdivide by proposing the zones of *A. capricornu* and *A. capitanei*, the former underlain by an unnamed horizon. *A. capitanei* is a Bean manuscript name based on an indeterminate fragment (Rawson 1970 : 591), and it is not clear which of the species described above in section IV is the intended index of the '*capricornu* Zone', though most of the specimens which Spath identified as *A. capricornu* belong to *A. bicarinatum*. For these reasons I have abandoned Spath's scheme and placed the whole of Bed C7 in the *Simbirskites* (*Speetoniceras*) *inversum* Zone (Rawson 1971a, 1971b). *Aegocrioceras* appears suddenly, and in abundance, in Bed C7G, about 0·3 m above the first appearance of *S.* (*Sp.*) *inversum*, and remains the dominant ammonite through the rest of C7. A *Speetoniceras* was chosen as zonal index because, despite the abundance of *Aegocrioceras*, the appearance of the latter genus represents a short-lived incursion into a region generally dominated by *Simbirskites* (Rawson 1973 : fig. 4). Two discrete *Aegocrioceras* assemblages were noted, a lower one of relatively inflated species in Beds C7G and C7F, followed by a group of more compressed forms in C7E–C7A (Rawson 1971b : 70). The difference in whorl section of the two groups is brought out by the break between species with a mean *wt/wh* ratio of 0·96–0·91 and those with mean ratio 0·78–0·67 (Table 1, p. 134).

The range and relative abundance of *Aegocrioceras* species in Bed C7 is summarized in Fig. 2. This clearly shows that the younger of the two assemblages previously recorded can be split, so that a total of three assemblages may be recognized. Although they are of clear stratigraphical significance they are not given the status of subzones here, since the faunal sequence is probably condensed and incomplete (see below).

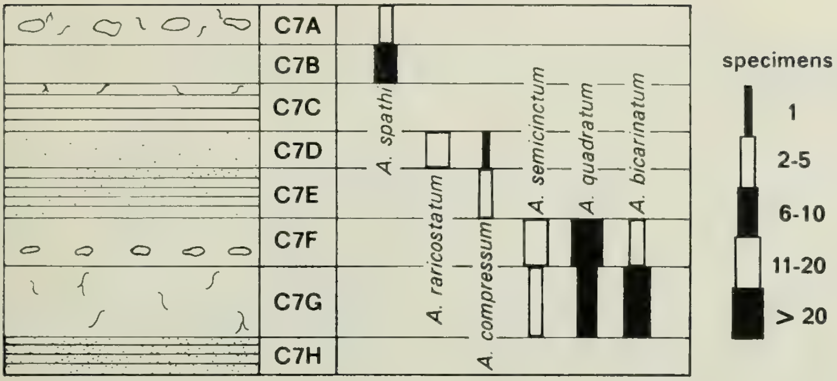

FIG. 2. Range and abundance of *Aegocrioceras* species in Bed C7, Speeton.

Assemblage 1 consists of the relatively stout-whorled species *A. semicinctum, A. quadratum* and *A. bicarinatum*, and is confined to Beds C7G and C7F.

Assemblage 2 contains *A. raricostatum* and *A. compressum*, though the former species is the dominant form. Both are considerably more compressed than members of Assemblage 1. Assemblage 2 is confined to Beds C7E and C7D.

Assemblage 3 consists of a single species, *A. spathi*, which occurs in Beds C7B and C7A (Bed C7C has not yielded *Aegocrioceras*). The first *Crioceratites* appear with late *A. spathi* in Bed C7A.

The rapid changes in distinct faunal assemblages through only 2·6 m of clay suggest a very condensed sedimentary sequence. This is also indicated by lithological evidence: *Chondrites* burrows, abundant glauconite (C7E), rapid colour changes and the occurrence of partially phosphatized nodules (in C7F and C7A) are all characteristic of interrupted or slow deposition. Furthermore, the equivalent beds are often much expanded in thickness in the Lower Saxony Basin in north Germany.

The relatively condensed nature of the Speeton succession implies that the preserved fauna may not reflect the whole spectrum of *Aegocrioceras* forms; *A. capricornu* is certainly absent. This makes it difficult to postulate an evolutionary lineage, though a possible one is summarized in Fig. 3. The lineage requires testing by further work on the north German faunas.

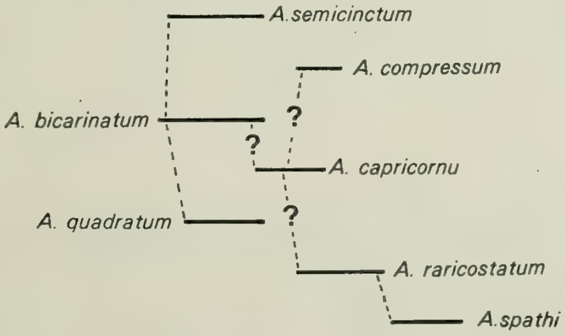

FIG. 3. Possible evolutionary lineages in *Aegocrioceras*.

VI. COMPARISON WITH OTHER *AEGOCRIOCERAS* FAUNAS

Aegocrioceras faunas are known from two other regions, the North Sea island of Heligoland and the Lower Saxony Basin of the north German mainland.

Heligoland. Lower Cretaceous clays crop out on the sea floor east of the main island ('Hauptinsel') of Heligoland, and ammonites washed up on the northern shore of the adjacent islet of Düne were first described by Roemer (1841). Heligoland and Speeton are, jointly, type localities for three species proposed by Roemer and now attributed to *Aegocrioceras*, namely '*Hamites*' *semicinctus*, '*H.*' *capricornu* and '*H.*' *subnodosus*. Koenen (1904) added *A. torulosum* (Koenen 1902) [= *A. quadratum* Crick 1898] and *A.* ? *seeleyi* (Neumayr & Uhlig) to the Heligoland records, and Hiltermann & Kemper (1969) figured *A. bicarinatum* (Young & Bird) and *A.* ? *koeneni* Spath.

Recently, skin-divers have collected about 100 *Aegocrioceras* loose from the sea floor, along with many other Lower Cretaceous ammonites (Kemper *et al.* 1974). The *Aegocrioceras* fauna is discussed in detail elsewhere (Rawson *in* Kemper *et al.* 1974; Rawson 1974); in both species content and preservation it is remarkably similar to that of the Speeton Clay, even to *A. quadratum* and *A. semicinctum* occurring as partially phosphatized body chambers or in phosphatic nodules – the preservation characteristic of the same species in Bed C7F at Speeton.

The new collections confirm the occurrence of *A. quadratum*, *A. bicarinatum*, *A. semicinctum*, *A.* ? *koeneni* and *A.* ? *seeleyi*, and add *A. spathi* and *A. raricostatum* to previous records. Thus the only Speeton species not represented from Heligoland are *A. compressum* and *A. densiradiatum*.

The Lower Saxony Basin. The stratigraphy, palaeontology and regional distribution of Lower Cretaceous sediments in the Lower Saxony Basin are extensively reviewed by Thiermann & Arnold (1964), Schott *et al.* (1967, 1969) and Kemper (1973a, 1973b). Through much of the Lower Cretaceous clays accumulated in the main part of the basin, and the central basin facies consists mainly of dark, shaley clays with bands of red-weathering, ferruginous concretions. The shallower-water and marginal facies are more varied, with sandstones, limestones and ironstones developed.

The abundance of *Aegocrioceras*, especially in argillaceous sediments, led to the recognition of an *A. capricornu* Zone (Koenen 1902) which is customarily taken as the base of the German Upper Hauterivian. Riedel (*in* Gürich & Dacque 1942) attempted to subdivide the zone but his subdivisions are difficult to uphold (e.g. Zedler 1959) and recent authors have reverted to a simpler *capricornu* Zone. The definition of this has varied, some authors including in it beds with early *Simbirskites* (the 'Obere *capricornu*-Zone') above the main *Aegocrioceras* horizon. Kemper (1973a) has proposed the term '*Aegocrioceras* spp. Zone' for the limited *capricornu* Zone; this correlates with the vertical distribution of *Aegocrioceras* (excluding *A.* ? *seeleyi* and *A.* ? *koeneni*) at Speeton.

The rich fauna of the *Aegocrioceras* Zone has never been adequately described though some species were described and figured by Neumayr & Uhlig (1881) and Koenen (1902). The numerous specimens in museum collections indicate that all three Speeton assemblages occur, especially in some of the prolific temporary sections exposed during the digging of the Mitteland Canal (completed in 1938). At present, the zone is exposed *in situ* at Ovenstadt (near Petershagen) and Sarstedt (near Hanover).

At Ovenstadt, basin-facies shaley clays yield abundant, though usually fragmentary, specimens, often of large size. The *Aegocrioceras* Zone is at least 15 m thick here, but the *A. quadratum/bicarinatum/semicinctum* fauna of Assemblage 1 at Speeton has not been collected ; it presumably lies beneath the lowest exposed horizon. There is an upward passage into the *Simbirskites* (*Milanowskia*) *staffi* Zone. Because of their large size, representing growth stages more advanced than those preserved at Speeton, most *Aegocrioceras* from this locality are difficult to compare with Speeton forms ; the specimens in my collection are identified as *A. capricornu*, *A.* cf. *raricostatum*, *A. compressum* (Pl. 5, fig. 5) and *A.* cf. *spathi*, indicating Assemblages 2 and 3.

At Sarstedt, flattened *Aegocrioceras* (complete with shell) are abundant through about 3 m of clay, though three-dimensional specimens are rare. The latter are pyritized, with shell, and normally not more than about 50 mm in diameter, so that they can be compared directly with Speeton specimens. The earliest forms belong to *A. raricostatum*, representing Assemblage 2. This is replaced higher up by *A. spathi* (Pl. 4, fig. 5), which in turn gives way abruptly to *Simbirskites* of the *staffi* Zone (Rawson 1971a : 75). The absence of Assemblage 1 is puzzling, since there is no obvious stratigraphical break, but may be explained by preservation failure since the clays beneath the *Aegocrioceras* Zone are completely without ammonites for several metres.

The similarity in preservation of the Sarstedt and Speeton *Aegocrioceras* (and *Endemoceras* and *Simbirskites*) is mirrored by the lithological similarity, the clays at both localities being much more varied in colour and mineral content than the basin-facies sediments. The clays at Sarstedt were deposited in relatively shallow water on the flanks of a salt-stock.

At Gildehaus, near Bentheim, blocks of Gildehauser Sandstone from a temporary section have yielded flattened *Aegocrioceras* (see Kemper 1968 : pl. 3, fig. 2), among which I have identified *A.* sp. cf. *quadratum* (Kemper's figured specimen) and *A. raricostatum* (Bramer collection, author's collection).

VII. CONCLUSIONS

The main *Aegocrioceras* fauna of the Speeton Clay occurs in Bed C7, where three distinct assemblages can be recognized through only 2·6 m of clay. The sequence is condensed and may not represent the whole spectrum of *Aegocrioceras* species. Two further 'species', only provisionally retained in *Aegocrioceras*, probably occur together higher in the succession ; one, *A.* ? *koeneni*, may be the inner whorls of the other, *A.* ? *seeleyi*.

All but one of the species recorded from Speeton occur in north Germany, and all but two are known from Heligoland.

Of the 12 specific names previously published for *Aegocrioceras* species, two are regarded as uninterpretable and two others as junior subjective synonyms. Another two species are newly described in this paper. A full list of previously published names and their interpretation is given in Table 3. Many unpublished names and misidentifications were listed by Spath (1924); these are tabulated in the Appendix (below).

TABLE 3

Previously published specific names in *Aegocrioceras*, and their present interpretation

Specific name	Interpretation in this paper
bicarinatum Young & Bird 1828	*bicarinatum* Young & Bird 1828
bucklandi Buckland 1836	uninterpretable
capricornu Roemer 1841	*capricornu* Roemer 1841
densiradiatum Rawson 1970	*densiradiatum* Rawson 1970
koeneni Spath 1924	*koeneni* Spath 1924 (? = *seeleyi* Neumayr & Uhlig 1881)
quadratum Crick 1898	*quadratum* Crick 1898
varicostatum Phillips 1829	*varicostatum* Phillips 1829
seeleyi Neumayr & Uhlig 1881	*seeleyi* Neumayr & Uhlig 1881
semicinctum Roemer 1841	*semicinctum* Roemer 1841
subnodosum Roemer 1841	uninterpretable (? *bicarinatum* Young & Bird)
subseeleyi Spath 1924	*bicarinatum* Young & Bird 1828
torulosum Koenen 1902	*quadratum* Crick 1898

VIII. APPENDIX: SPATH'S (1924) FAUNAL LIST

Dr L. F. Spath examined the collections 'of many Public Museums and numerous private collectors' (Spath 1924 : 73) during the compilation of his exhaustive list of Speeton Clay ammonites : evidence within his paper shows that he saw collections in the British Museum (Natural History), the Geological Survey Museum (which already included the Danford collection), the Sedgwick Museum, Hull Museum, Scarborough Museum and the Yorkshire Museum, together with the private collection of G. W. Lamplugh now in the British Museum (Natural History). The Herries collection, subsequently transferred to the Yorkshire Museum, also bears some labels in Spath's handwriting, apparently predating his 1924 paper.

In attempting to list the whole of the Speeton Clay fauna Spath could not hope to provide a critical revision, so that it is hardly surprising that his tabulation of the *Aegocrioceras* fauna is a compilation of valid and invalid names, whose usage seems to vary from one collection to the next. Many of the extant collections which Spath examined bear little indication of his determinations, but the majority of the *Aegocrioceras* specimens in the Institute of Geological Sciences (formerly Geological Survey Museum) collections and a few of those in the British Museum (Natural History) have Spath identifications of proven pedigree. Thus his published records can be interpreted to a limited extent : Spath's 22 listed taxa are tabulated below, together with the catalogue numbers of specimens which he is known to have identified and their revised identification.

Spath's record	Cat. no.	Revised identification
A. bucklandi (Phillips) Buckland sp.	GSM. 32081	*A.* sp. indet.
A. bucklandi var. (Bean MS) (less compressed)	–	–
A. capitanei (Bean MS)	BM. C72670	*A.* cf. *varicostatum*
	GSM. 17495	*A. semicinctum*
	GSM. 32096	*A.* cf. *spathi*
A. sp. nov. aff. *capitanei* (Bean MS)	BM. C72704	*A. densiradiatum* (holotype)
	GSM. 17479	*A. densiradiatum*
	GSM. 17498	*A. densiradiatum* (paratype)
A. capricornu (Roemer)	BM. C72656–7	*A. bicarinatum*
A. cristatum Pavlow *non* d'Orb. sp.	–	–
A. aff. *cristatum* (Pavl. *non* d'Orb.)	GSM. 17478	*A.* aff. *bicarinatum*
	GSM. 32080	*A. bicarinatum*
A. intermedium (Phillips)	GSM. 17482, 17484–7, 17489, 17490, 17492, 17493, 32137	*A. varicostatum*
A. intermedium (Bean MS *non* Phillips)	BM. 89107	*A. bicarinatum* (neotype)
A. sp. nov ? aff. *intermedium* ('cf. *duvali*' Koenen *in* Danford)	GSM. 17475–6	*A.* cf. *bicarinatum*
A. koeneni sp. nov.	GSM. 32097	*A.* sp.
A. ligatum (Bean MS)	YM. 885, PR/1975/1	*A. semicinctum*
	BM. 89101	*A.* sp. indet.
A. quadratum (Bean MS) Crick sp.	BM. 89102, C7154	*A. quadratum* (syntypes)
A. varicostatum (Phillips)	–	–
A. seeleyi (Neumayr & Uhlig)	–	–
A. semicinctum (Roemer)	BM. C72653, GSM. 32090	*A. quadratum*
	GSM. 32074–5	*A.* cf. *quadratum*
	GSM. 17477, 17537, 32124	*A. bicarinatum*
A. cf. *semicinctum* (Roemer) (? = *insigne* Pictet)	–	–
A. sp. nov. ? aff. *semicinctum* (Roemer)	–	–
A. subnodosum (Roemer)	–	–
A. subseeleyi sp. nov.	GSM. 17540	*A. bicarinatum*
	YM. tablet 420	*A.* cf. *bicarinatum*
	GSM. 17499, 32143	*A.* sp. juv.
A. torulosum (Koenen)	BM. C72652	*A. quadratum*
A. sp. nov.	–	–

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PLATES 1–6

All photographs are by Mr B. J. Samuels of Queen Mary College. The specimens have been coated with ammonium chloride. All figures × 1, except Pl. 2, fig. 3.

PLATE 1

Aegocrioceras quadratum (Crick) (p. 140 ; see also Pl. 2, fig. 2 and Pl. 3, fig. 1)

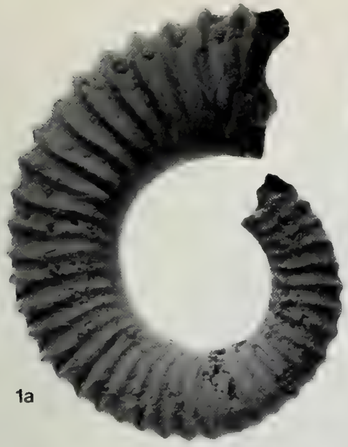
FIG. 1. Septate inner whorls from Bed C7G, Speeton. BM. C79040.

FIG. 3. Septate inner whorls from Bed C7G, Speeton. BM. C79041.

FIG. 4. Body chamber and associated inner whorls in a nodule from Bed C7F. The ventral part of each of the inner whorls is obscured by hard matrix so that the whorls appear more widely separated than they really are. BM. C78996 (collected by Mr M. K. Durkin during a Geologists' Association excursion, 1967).

Aegocrioceras bicarinatum (Young & Bird) (p. 138 ; see also Pl. 2, fig. 1)

FIG. 2. Septate inner whorls from Bed C7G, Speeton. BM. C78933.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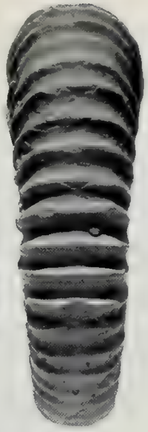
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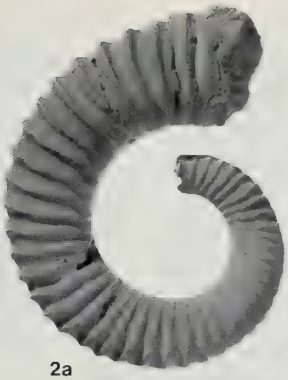
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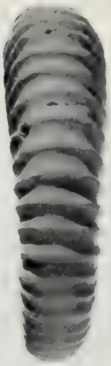
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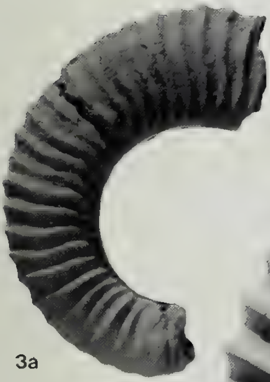
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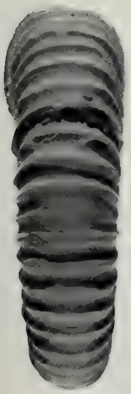
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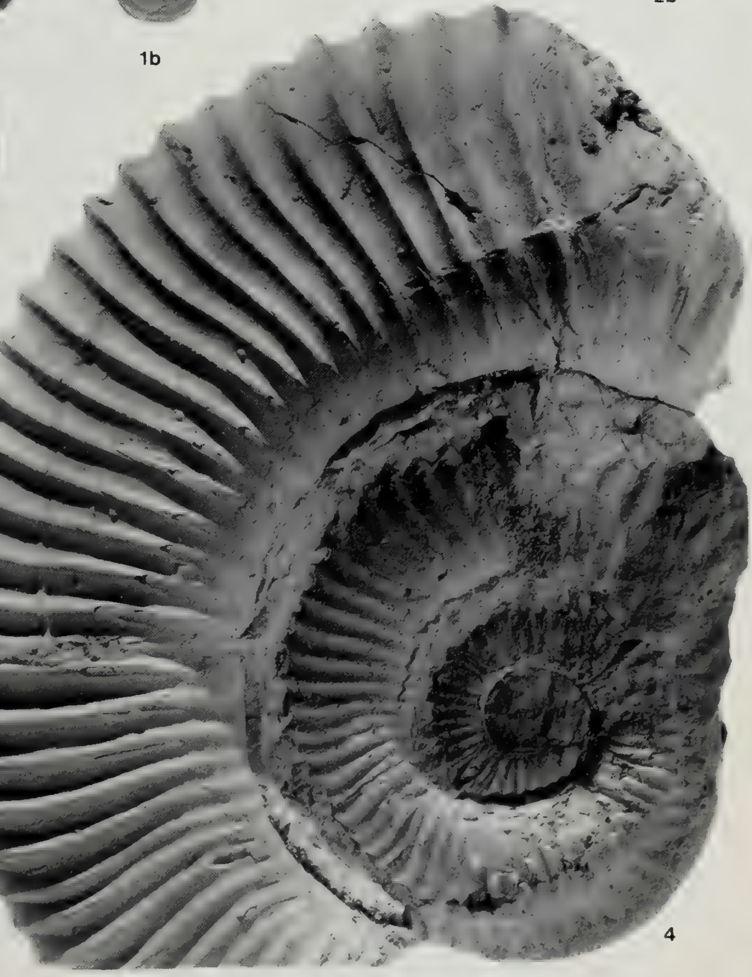
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PLATE 2

Aegocrioceras bicarinatum (Young & Bird) (p. 138 ; see also Pl. 1, fig. 2)

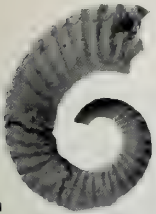
FIG. 1. C Beds, Speeton. An evolute variety, the lectotype of *A. subseeleyi* Spath. GSM. 17540 (Danford collection).

Aegocrioceras quadratum (Crick) (p. 140 ; see also Pl. 1, figs 1, 3, 4 and Pl. 3, fig. 1)

FIG. 2. Bed C7F, above the nodule horizon. A well-preserved body chamber with shell, presumably adult. BM. C79017.

Aegocrioceras semicinctum (Roemer) (p. 141 ; see also Pl. 3, figs 2, 3)

FIG. 3. Almost complete (adult ?) specimen with body chamber : stereo-pair × 0·7 to show the rounded flanks and tendency to form mid-lateral tubercles in the inner whorls. GSM. 22226 (Danford collection), in a nodule of C7F type.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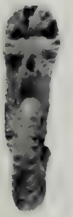
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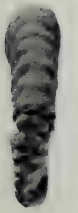
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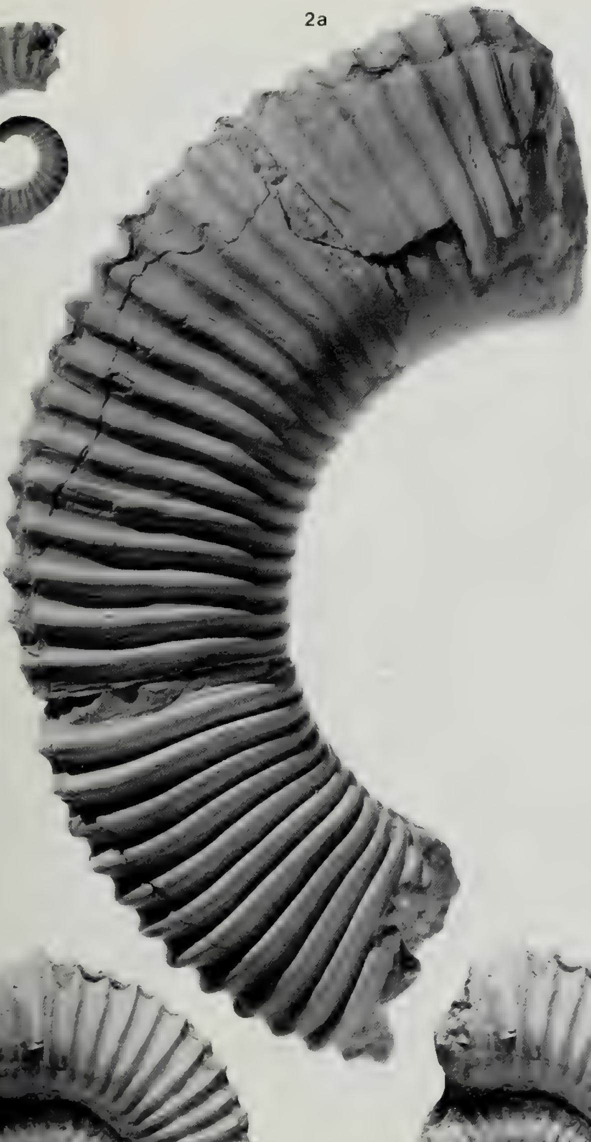
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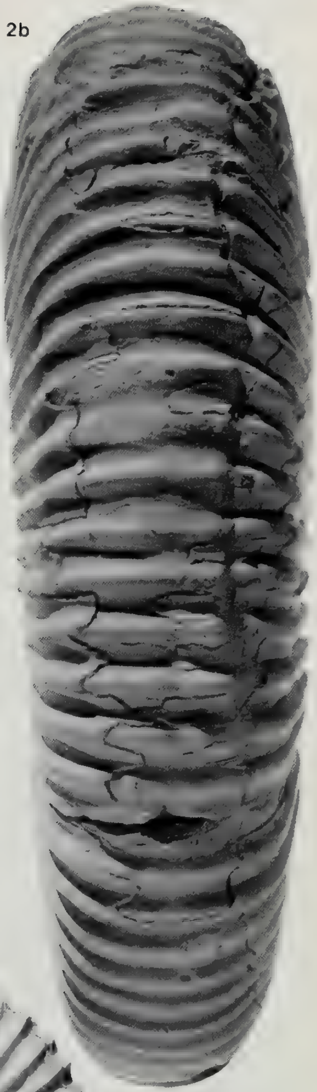
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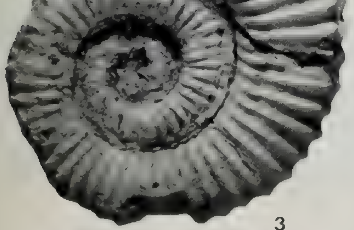
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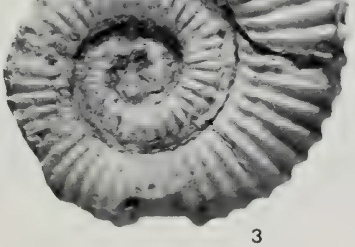
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PLATE 3

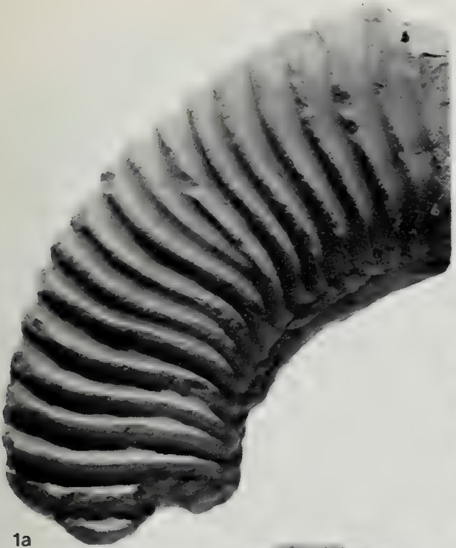
Aegocrioceras quadratum (Crick) (p. 140 ; see also Pl. 1, figs 1, 3, 4 and Pl. 2, fig. 2)

FIG. 1. Fragmentary body chamber of a moderately compressed example. *Aegocrioceras* Zone, Ziegelei Osterwald, north-west of Hanover. GPiG. (uncatalogued).

Aegocrioceras semicinctum (Roemer) (p. 141 ; see also Pl. 2, fig. 3)

FIG. 2. Bed C7F, Speeton. Body chamber and last few air chambers of one of the largest known examples. BM. C78954.

FIG. 3. Almost complete (adult ?) specimen with body chamber : a typical form with rursiradiate ribs, bearing William Bean's original label '*Crioceratites ligatus*'. YM. 885 (Bean collection), in a nodule of C7F type.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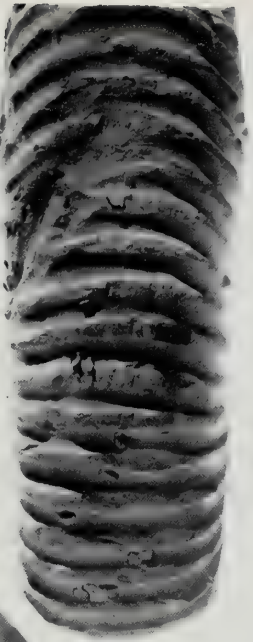
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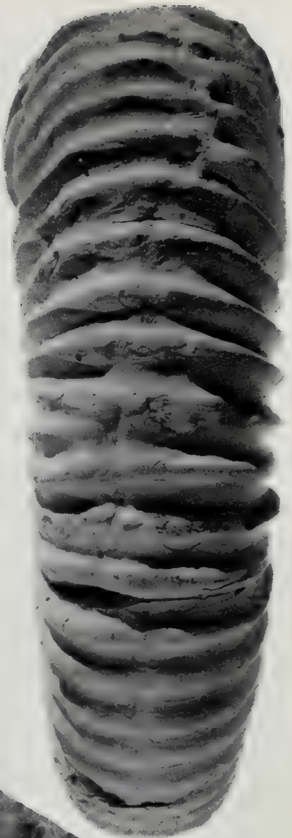
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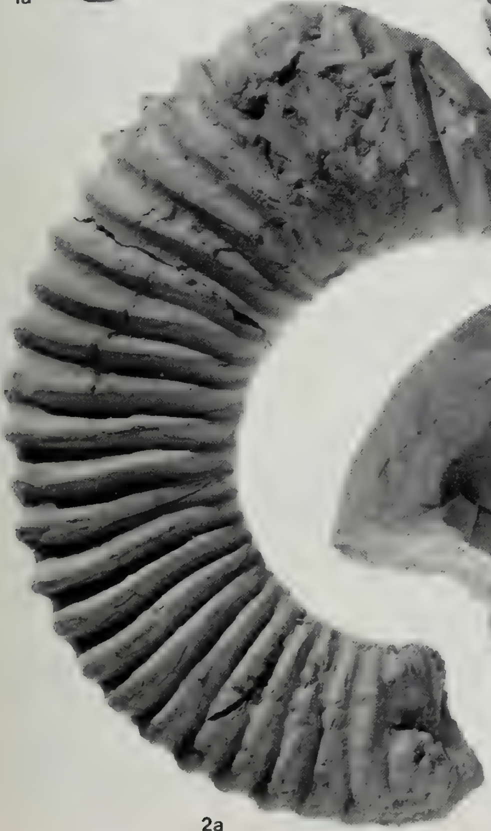
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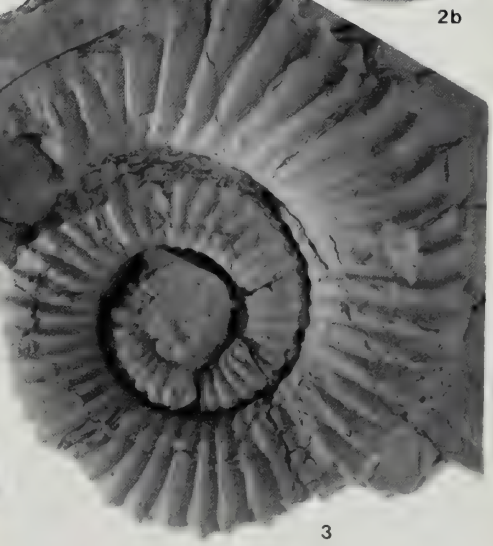
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PLATE 4

Aegocrioceras spathi sp. nov. (p. 145)

FIG. 1. Paratype, a slightly crushed specimen with shell preserved, showing the degree of uncoiling. Bed C7A, Speeton. BM. C78985.

FIG. 2. Holotype. An undistorted specimen showing the posterior curvature of the ribs over the venter. Speeton, loose but in a red siltstone matrix matching that of Bed C7A. BM. C78978.

FIG. 5. Paratype. Slightly distorted whorl from the upper part of the *Aegocrioceras* Zone, Sarstedt, near Hanover. NLfB. Kh.66.

Aegocrioceras ? koeneni Spath (p. 149 ; see also Pl. 5, fig. 5)

FIG. 3. Neotype. Speeton, exact horizon unknown. HU. Neale collection S1731.

FIG. 4. The largest known specimen, showing the sharp forward curvature of the ribs towards the venter and the feeble ventro-lateral swellings. Speeton, exact horizon not known. Wrights' collection 19253.

Aegocrioceras raricostatum (Phillips) (p. 143 ; see also Pl. 5, figs 3, 4, 7)

FIG. 6. Showing the slow increase in whorl height. Speeton, exact horizon not known. GSM. 17449 (Danford collection).

FIG. 7. A variant with rounded whorl section, bearing William Bean's original label '*Hamites rotundus* Phillips'. Speeton, horizon unknown. BM. 89106 (Bean collection).

FIG. 8. Speeton, exact horizon not known. HM. 22/64/12.

FIG. 9. A variant with rounded whorl section. Bed C7D, Speeton. BM. C78964.

FIG. 10. A large example of the variant with round whorl. Speeton, with loose label 'B Beds', BM. C72671 (Lamplugh collection).

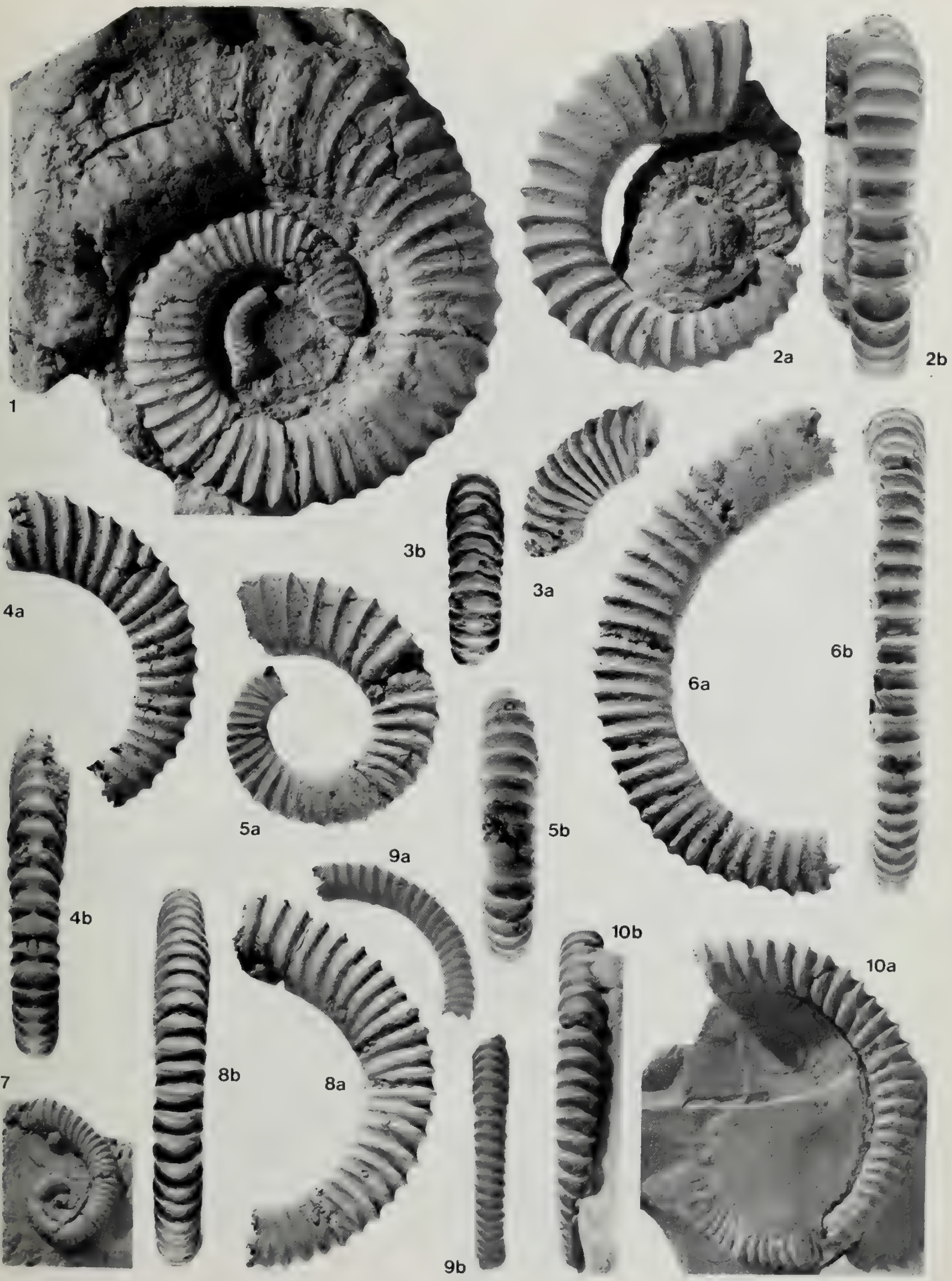

1
2a
2b
3b
3a
4a
6b
6a
5a
5b
9a
4b
10b
10a
7
8b
8a
9b

PLATE 5

Aegocrioceras capricornu (Roemer) (p. 147)

FIG. 1. *Aegocrioceras* Zone, Ziegelei Osterwald, NNW of Hanover. GPiG. (uncatalogued).

Aegocrioceras compressum sp. nov. (p. 144)

FIG. 2. Holotype. Bed C7D, Speeton. BM. C78974.

FIG. 6. Paratype. *Aegocrioceras* Zone, Ovenstadt, near Petershagen. The whorl section is across the line of breakage in the middle of the specimen. NLfB. Orig.-nr. Kh.68 (collected by the author).

Aegocrioceras raricostatum (Phillips) (p. 143 ; see also Pl. 4, figs 6–10)

FIG. 3. Fragment with widely spaced ribs closely matching Phillips' sketch of the lost holotype. Bed C7. Wrights' collection 20392.

FIG. 4. A variant in which the ribs are practically straight on flanks and venter. Mitteland Canal, near Idensen (south-west of Wunstorf). NLfB. Orig.-nr. Kh.67.

FIG. 7. Neotype, a slightly distorted whorl showing the feeble backward curvature of the ribs over the venter. Bed C7D, Speeton. BM. C78963.

Aegocrioceras ? koeneni Spath (p. 149 ; see also Pl. 4, figs 3, 4)

FIG. 5. Finely ribbed variety. Speeton, exact horizon not known. BM. C72171 (W. T. Dean collection).

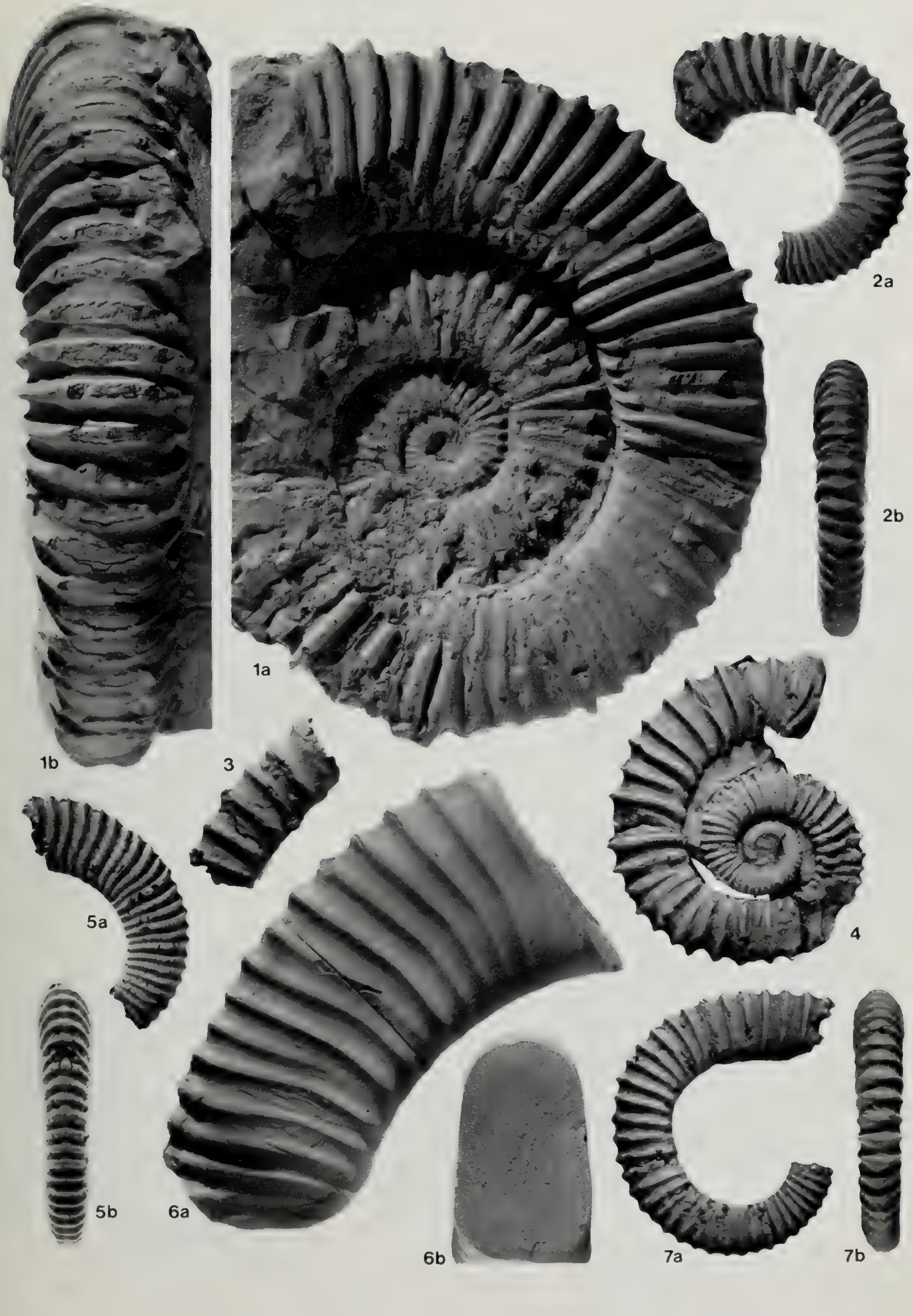

1a
1b
2a
2b
3
4
5a
5b
6a
6b
7a
7b

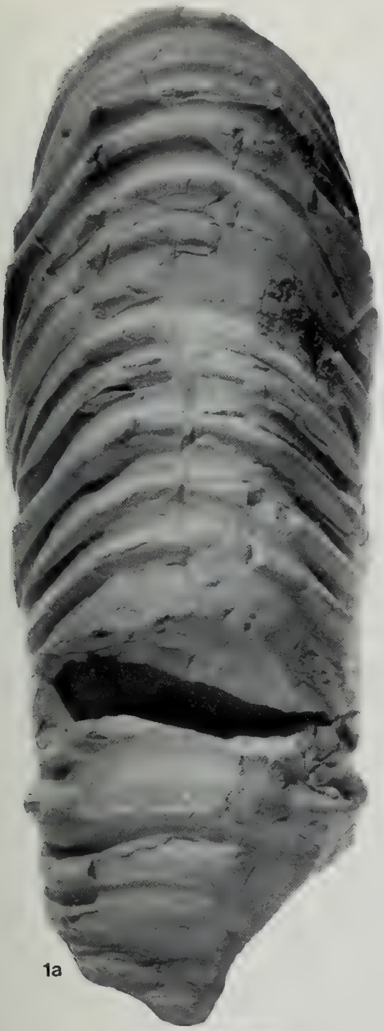
PLATE 6

Aegocrioceras ? seeleyi (Neumayr & Uhlig) (p. 148)

FIG. 1. Body chamber from Bed C4L, Speeton. Variant with small, mid-lateral tubercles. BM. C78988.

Aegocrioceras densiradiatum Rawson (p. 146)

FIG. 2. Holotype. Speeton Clay, horizon not known. BM. C72704 (Bean collection).



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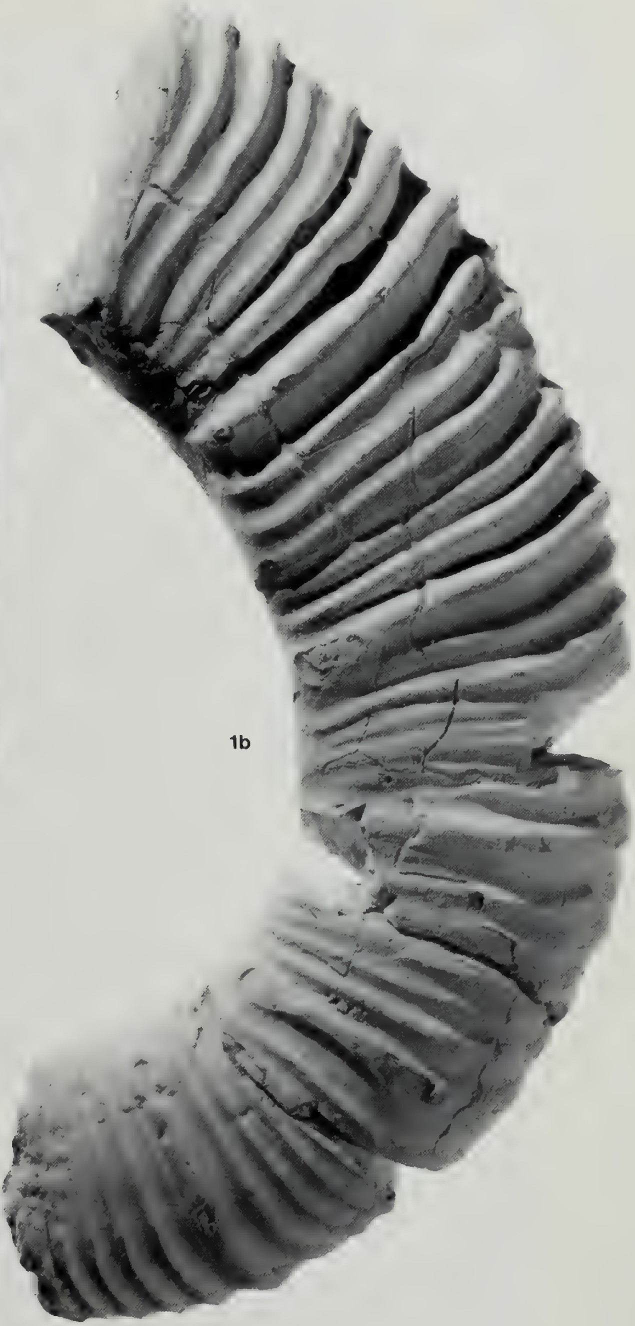

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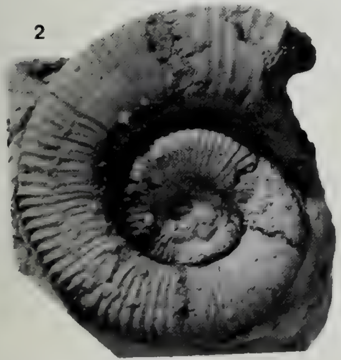

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OSTRACODS FROM CALLOVIAN TO TITHONIAN SEDIMENTS OF TANZANIA, EAST AFRICA

R. H. BATE

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THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 26 No. 5
LONDON : 1975

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BY

RAYMOND HOLMES BATE

Pp 161–223 ; 14 *Plates* ; 22 *Text-figures*

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GEOLOGY Vol. 26 No. 5
LONDON: 1975

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OSTRACODS FROM CALLOVIAN TO TITHONIAN SEDIMENTS OF TANZANIA, EAST AFRICA

By RAYMOND HOLMES BATE

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ABSTRACT

The Upper Jurassic ostracod fauna of Tanzania is described and shown to comprise five distinct faunal assemblages each characterized by a species of *Majungaella*. Fifty-two ostracod species are recognized of which 24 are new. Four new genera, *Amicytheridea*, *Afrocytheridea*, *Mandawacythere* and *Rhadinocythere*, are described. Twenty species are retained under open nomenclature. The ostracod fauna of Tanzania is compared with that described from Madagascar, India and South Africa. At the present time two known species are common to Tanzania and South Africa, eight to Tanzania and Madagascar and five to Tanzania and India (Kutch). Fourteen are common to India and Madagascar. Incomplete sampling or lack of exposures is considered to be responsible for this numerical variation. It is anticipated that further investigations will add to the list of species common to these countries. One ostracod is also common to Tanzania and Western Australia.

The Tanzanian sequence appears to have been deposited in a shallow water, continental shelf environment ; closeness of land is evidenced by the presence of freshwater ostracods in the Middle Callovian of the Mandawa sequence.

Of the 28 ostracod genera recorded, seven are known only from the southern hemisphere (this presumes a pre-drift location for India) ; the remainder are cosmopolitan.

I. INTRODUCTION

The present research was stimulated by the receipt, from the Geological Survey of Tanganyika, of a series of samples collected through the Jurassic and Cretaceous by the field geologist W. R. Moore. The examination of this material showed that additional field collecting was necessary and an expedition to Tanzania was mounted in the summer of 1965, by the Department of Palaeontology jointly with the Geological Survey of Tanganyika.

Three regions were examined in detail : the Wami River Area, north of Dar-es-Salaam, the Central Railway Area to the south-west and the Mandawa Anticline in the south (Text-fig. 1).

The Wami River Area and the Mandawa Anticline both yielded good Upper Jurassic microfaunas but the Middle Jurassic proved to be completely barren. Exposures were not common and were largely restricted to dry stream banks, the

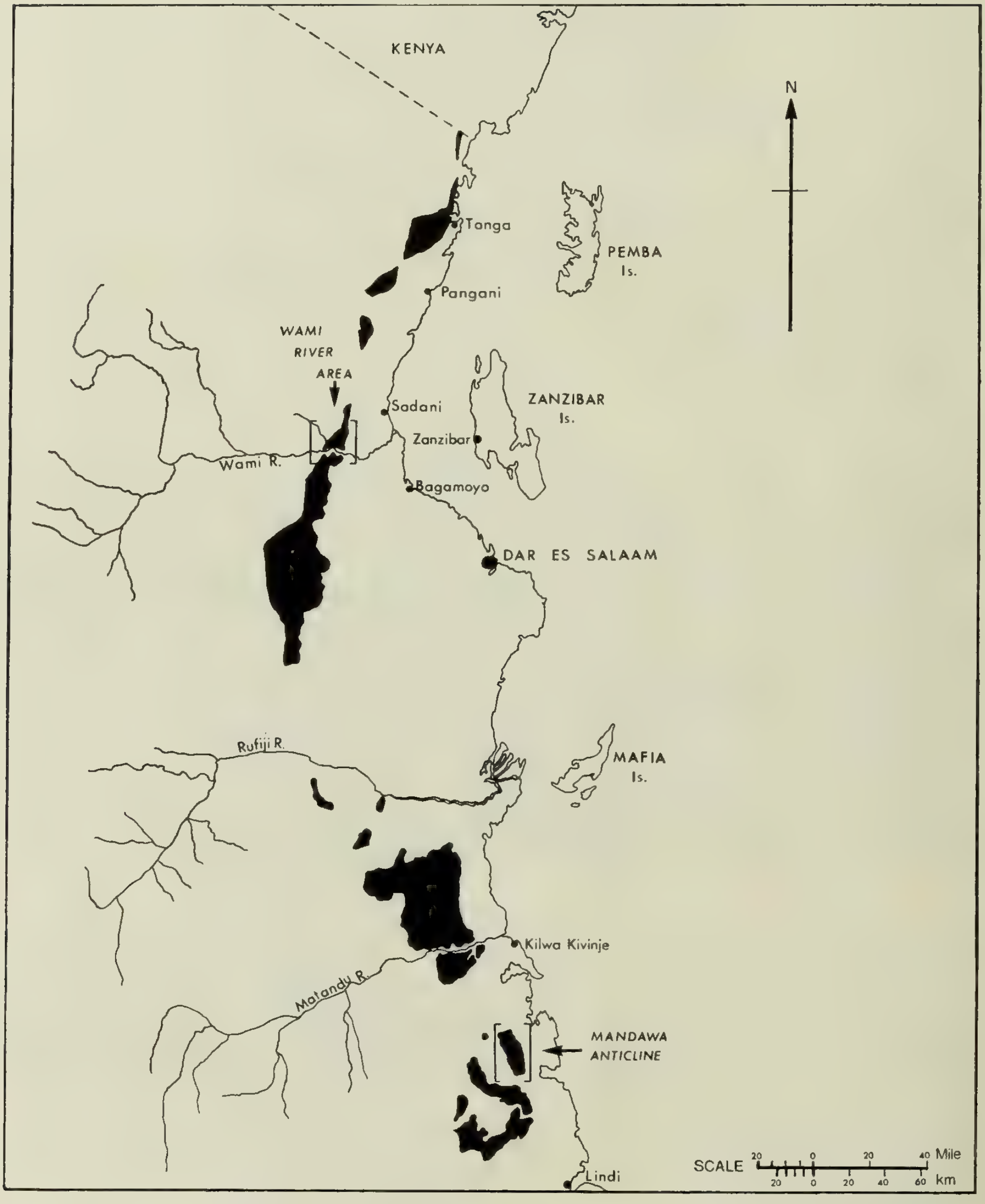
KENYA
N
Tonga
PEMBA Is.
Pangani
WAMI RIVER AREA
Sadani
ZANZIBAR Is.
Zanzibar
Wami R.
Bagamoyo
DAR ES SALAAM
Rufiji R.
MAFIA Is.
Kilwa Kivinje
Matandu R.
MANDAWA ANTICLINE
Lindi
SCALE
20 0 20 40 Mile
20 0 20 40 60 km

FIG. 1. Map of Tanzania to show localities and distribution of Jurassic outcrop (black).

intervening terrain being covered by thorn scrub, grassland or cultivation. The Central Railway Area was entirely unproductive and is not dealt with further. There has been no previous work undertaken on the Jurassic ostracods of Tanzania but they have been described from Madagascar (Grekoff 1963), the Majunga Basin of which appears to mirror the sediments developed in Tanzania. Although Grekoff described forty-nine ostracods in his paper only a few have so far been recognized in Tanzania. The most important of these is the genus *Majungaella*, a close relative of the European Jurassic genus *Progonocythere* Sylvester-Bradley 1948. The stratigraphical importance of *Majungaella* will be discussed later.

In addition to East Africa and Madagascar, Jurassic ostracods have been described from South Africa (Dingle 1972) and from north-west India (Ljubimova, Guha & Mohan 1960 and Guha 1975?), some species of which are common to Tanzania and from off Western Australia (Oertli 1974).

The purpose of this paper is to describe the ostracod faunas obtained from the Upper Jurassic of Tanzania and to discuss their value in correlation both within Tanzania and between other countries in the region surrounding the Indian Ocean. A preliminary paper outlining the ostracod faunal assemblages of the Tanzanian Upper Jurassic was read in Tunis (6th African Micropalaeontological Colloquium, April 1974). Subsequently a number of changes concerning the dating of the samples became necessary. The most up-to-date information is presented here.

II. STRATIGRAPHY

The Wami River Area

The geology of this region (Text-fig. 2) was published as a geological map (Quarter Degree Sheet 168) of the Bagamoyo District (Moore 1963). This map covers most of the area examined although it omits the Msata-Masugulu region in the west. Moore records some 1100 m (3600 ft) of sediment belonging to the Upper Jurassic of which 810 m (2650 ft) is dated as Upper Oxfordian – the remainder is not specified. Of the Jurassic outcrop 122 m (400 ft) is identified as Middle Jurassic.

This paper shows that definite Middle Callovian (*anceps* Zone) underlies a thick Upper Oxfordian succession. The Middle Jurassic proved to be devoid of microfossils ; indeed, the arenaceous nature of the Jurassic sediments (sandy shales, sandstones and sandy limestones) has almost certainly contributed towards their absence through decalcification. Thus although Middle Callovian, Upper Oxfordian and Middle Jurassic sediments have been identified, the absence of the remaining part of the succession is more likely to be the result of lack of exposures than of non-deposition. Exposures are largely limited to dry streams with minor exposures along the banks of the Wami River in road tracks and excavations.

The following productive samples are listed in descending stratigraphical order ; those prefixed 'BM' were collected by the Survey geologist W. R. Moore and those prefixed 'B' during the Museum Expedition in 1965. (Because the scale used for the eastings differs from that for the northings on the Ordnance Survey maps of Tanzania the grid references are given with four digits East and five digits North.)

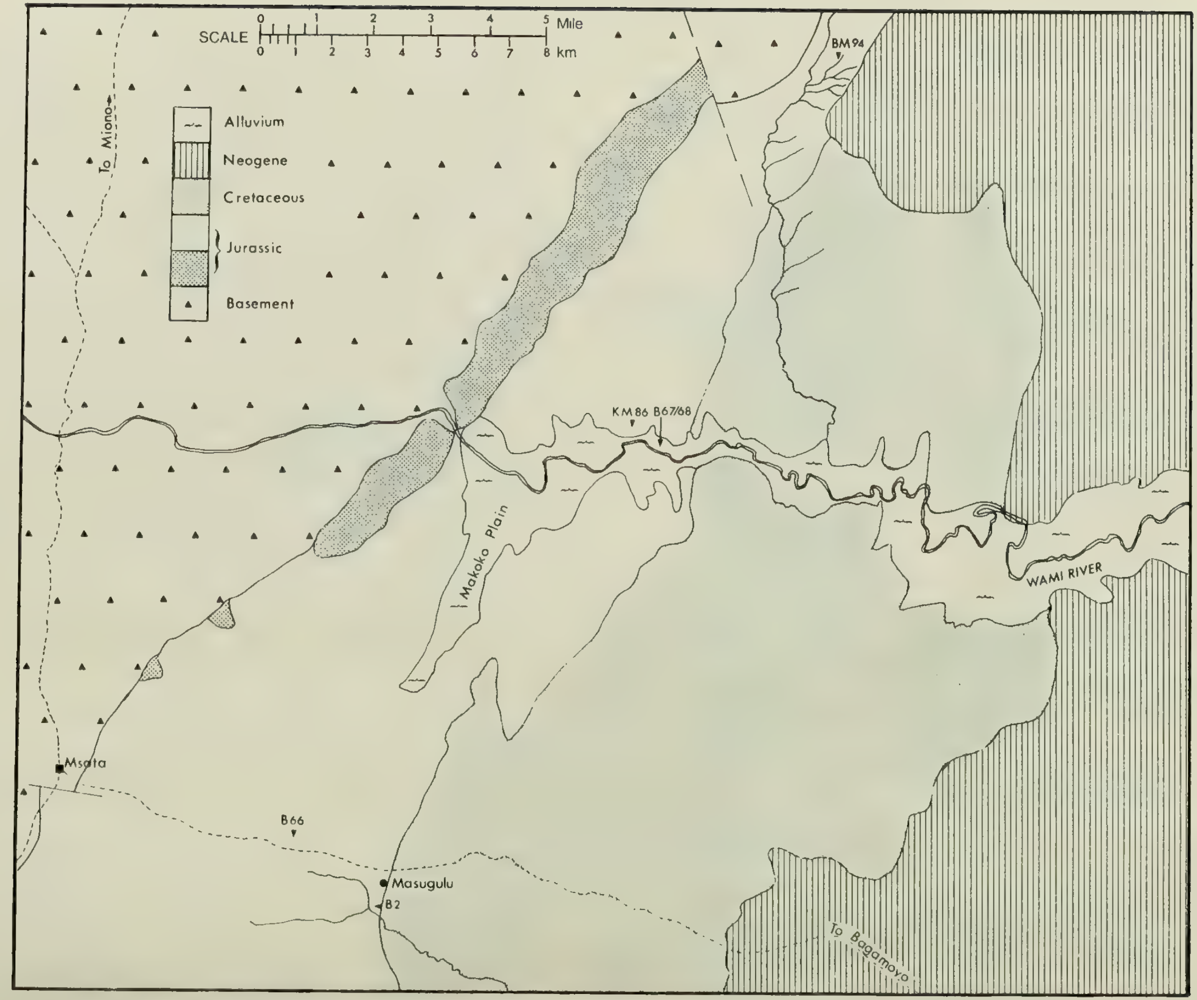
SCALE
0 1 2 3 4 5 Mile
0 1 2 3 4 5 6 7 8 km
Alluvium
Neogene
Cretaceous
Jurassic
Basement
To Miono
BM94
KM86
B67/68
Makoko Plain
WAMI RIVER
Msata
B66
Masugulu
B2
To Bagamoyo

FIG. 2. Map of Wami River Area to show location of samples. Based on unpublished Tanganyika Survey Map.

UPPER OXFORDIAN. BM50, B68–67 : micaceous siltstone exposed on the northern bank of the Wami River opposite the village of Lugoba Kinguli. Ordnance Survey Sheet 168/I ref : 4491E 93095N.

BM86 : mudstone exposed on the slip face of small hill on the northern side of Wami River. O.S. Sheet 168/I ref : 4483E 93102N.

B2 : grey shale exposed on north side of dam 0·4 km ($\frac{1}{4}$ ml) due south of Masugulu village. Dated on ammonites as belonging to the lower half of the Upper Oxfordian *transversarium* Zone (= *plicatilis* Zone of England) ; O.S. Sheet 167/IV ref : 4413E 92963N.

The index ostracod *Majungaella oxfordiana* sp. nov. is not present in all samples but by correlating B2 and B67 it would appear that the entire sequence of Oxfordian sediments is of Lower Upper Oxfordian age.

MIDDLE CALLOVIAN. BM94 : black silty clay exposed in a stream section north of the Wami River. O.S. Sheet 168/I ref : 4538E 93200N.

B66 : grey shale exposed 0·4 km ($\frac{1}{4}$ ml) north of the Msata–Bagamoyo road 4·0 km ($2\frac{1}{2}$ ml) west of Masugulu village in a small stream section cutting through a maize field. Nodules overlying the shale contain ammonites of the Middle Callovian *anceps* Zone. O.S. Sheet 167/IV ref : 4391E 92987N.

The Mandawa Anticline

This area (Text-fig. 3) has been investigated in detail by Aitken (1961) and although all stages of the Middle and Upper Jurassic are reported as being present the succession is not continuous. Aitken also states that below the Callovian the fossils are neither abundant nor diagnostic. Certainly no microfossils were found below the Callovian ; the Pindiro Shale which forms the centre of the anticline and which is questionably of Bajocian age was disappointingly barren.

Aitken records a maximum thickness of 1200 m (3930 ft) for the Upper Jurassic and over 275 m (900 ft) for the Middle Jurassic.

Exposures are, as in the Wami River Area, largely restricted to dry stream beds and even so are not common. Furthermore, the high proportion of arenaceous material has ensured that decalcification of the surface outcrop has largely removed the microfossils. A large proportion of the samples collected therefore proved to be barren. The following contained good faunas and are listed in descending stratigraphical order :

TITHONIAN. B110–111 : brown and green marl interbedded with thin siltstone bands exposed in the right bank of the Nalwehe stream, just below Aitken locality 2179. This horizon is high in the Tithonian sequence and, according to Dr N. J. Morris (personal communication), could even be Berriasian in age. A precise age is not assignable, however, and an Upper Tithonian dating would appear to be acceptable. This is to some extent confirmed by the presence of the Tithonian ostracod *Majungaella perforata* Grekoff and the absence of the Tithonian–Lower Cretaceous *Majungaella nematis* Grekoff, but no categorical statement concerning the age is possible at this time.

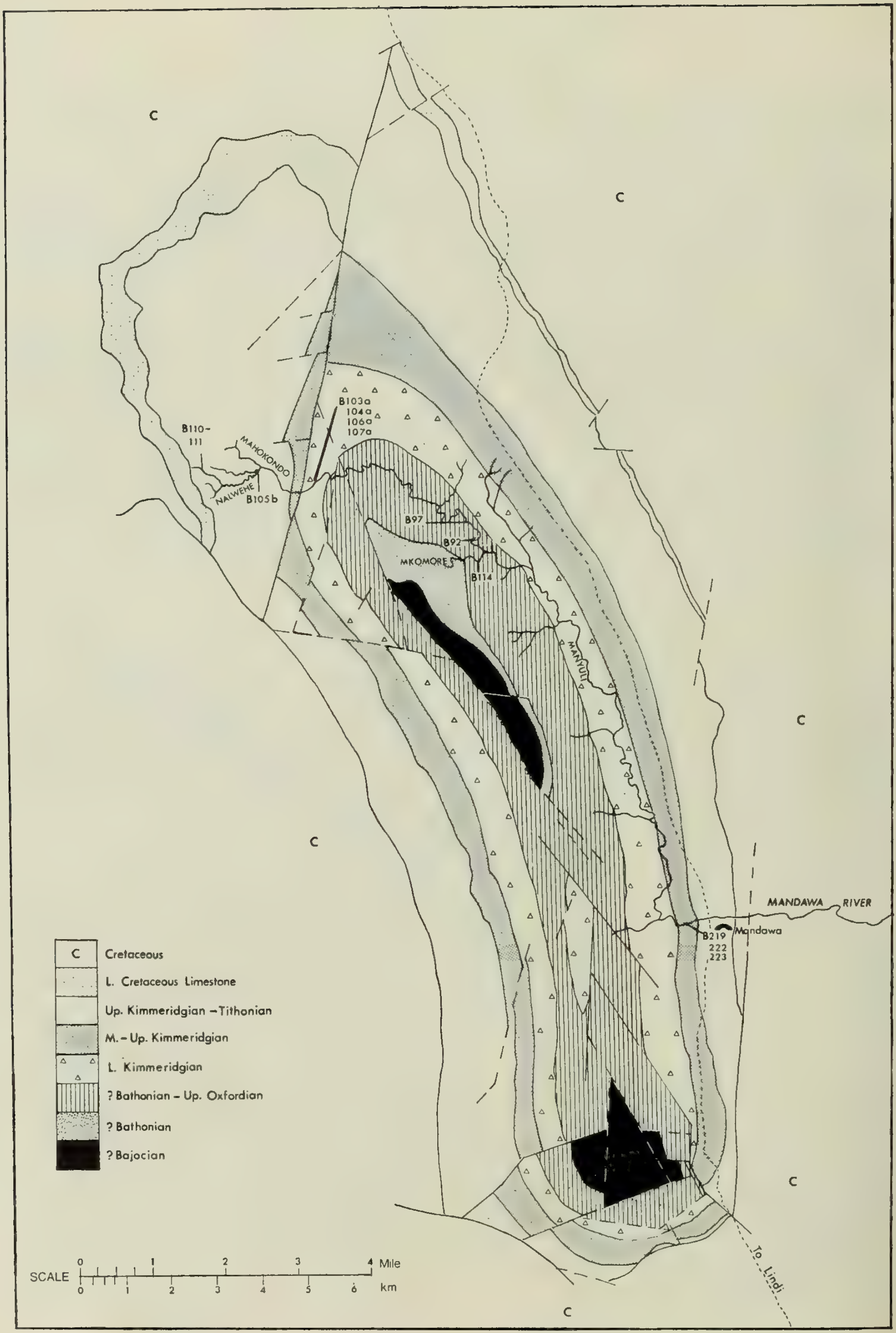
C
C
B103a
104a
106a
107a
B110-
111
MAHOKONDO
NALWEHE
B105b
B97
B92
MKOMORE
B114
MANYULI
C
C
MANDAWA
RIVER
B219
222
223
Mandawa
C
To Lindi
C
C Cretaceous
L. Cretaceous Limestone
Up. Kimmeridgian – Tithonian
M. – Up. Kimmeridgian
L. Kimmeridgian
? Bathonian – Up. Oxfordian
? Bathonian
? Bajocian
SCALE
0
1
2
3
4
Mile
0
1
2
3
4
5
6
km

FIG. 3. Map of Mandawa Anticline to show location of samples. After Aitken (1961).

B105B : buff siltstone with interbedded siltstone nodules, exposed about 1·6 km (1 ml) downstream from B110–111 ; Nalwehe stream. The most accurate dating here would be (?) Lower Tithonian.

MIDDLE OR UPPER KIMMERIDGIAN. B219–223 : grey silty shale exposed on left bank of the Mandawa River just upstream of Mandawa village ; Aitken locality 794. It is not possible to be more precise concerning the age of this sequence which occurs above the level dated as Middle or Upper Kimmeridgian by Aitken (1961), from which he obtained the bivalves *Trigonia* (*Indotrigonia*) *mandawae* and *T.* (*Indotrigonia*) *tanganyicensis*, and below the Tithonian horizon of his *T.* (*Indotrigonia*) *vstriata* and *T.* (*Indotrigonia*) *africana*.

LOWER KIMMERIDGIAN. B103a–107a : dark grey shale with siltstone nodules exposed in high left bank of the Manyuli stream 183 m (200 yds) west of Aitken locality 2159. This sequence, which is particularly well exposed, has been accurately dated on associated ammonites as Lower Kimmeridgian.

MIDDLE CALLOVIAN (*anceps* Zone = B66 and BM94 of the Wami River Area). B92 : buff sandy limestone weathering to yellow sandstone, shelly and oolitic. Aitken locality 2219 ; Manyuli stream.

B97 : grey sand shales with thin sandstone bands, some with shells. Right bank of the Manyuli stream.

B114 : greenish-buff soft flaggy sandstone containing shells, exposed in right bank of the Mkomore stream.

III. SYSTEMATIC DESCRIPTIONS

All specimens described have been deposited in the collections of the Palaeontology Department, British Museum (Natural History). Unless otherwise stated, the number of specimens recorded for each species refers only to those separately mounted and catalogued. Additional material is available in the faunal slide collection.

Order PODOCOPIDA Müller 1894

Suborder PLATYCOPINA Sars 1866

Family **CYTHERELLIDAE** Sars 1866

Genus ***CYTHERELLA*** Jones 1849

Cytherella cf. ***collapsa*** Grekoff 1963

Pl. 1, fig. 11

MATERIAL. A single specimen, Io.5821, sample B66.

HORIZON AND LOCALITY. Middle Callovian ; sample B66, Wami River Area, north of the Msata–Bagamoyo road (Text-fig. 2).

DISCUSSION. Grekoff records *Cytherella collapsa* from the Middle Callovian of Madagascar. In Tanzania a form very close to *C. collapsa* commonly occurs in the Middle Callovian but differs in having the median constriction of the carapace, as seen in side view, less positively developed. *C. collapsa* also tends to be more broadly rounded at its posterior end than does the Tanzanian material although variations here suggest that this may not be significant. At this time it is preferred not to identify the Tanzanian species directly with *C. collapsa*, but when the range of variation becomes known this may be necessary.

Dimensions. Io.5821, left valve (Pl. 1, fig. 11), length 0·64 mm ; height 0·32 mm.

Cytherella knysnaensis Dingle 1972

Pl. 1, figs 1, 5

1972 *Cytherella knysnaensis* Dingle : 289 ; pl. 15f–h.

Material. Two specimens, Io.6021–2, sample B97.

Horizon and Locality. Middle Callovian ; samples B92 and B97, Manyuli stream and sample B114, Mkomore stream, Mandawa Anticline (Text-fig. 3).

Discussion. *Cytherella knysnaensis* is associated in the Callovian of the Knysna outlier (Cape Province, South Africa) with *Cytherelloidea brentonensis* Dingle. The marine facies containing these ostracods is interbedded with non-marine sediments and Dingle considers the sequence to represent a near-shore environment. In the Mandawa Anticline *Cytherella knysnaensis* is also associated with *Cytherelloidea brentonensis*, together with *Darwinula* sp. and charophytes, indicating a near-shore environment with some freshwater influence.

Further north in the Wami River Area the Callovian appears to be more marine and here the species of *Cytherella* are *C. masuguluensis* sp. nov. and *C.* cf. *collapsa* Dingle. Possibly the change in the species present is a reflection on the environment, the northern outcrop representing more saline conditions.

Dimensions. Io.6021, carapace (Pl. 1, fig. 1), length 0·80 mm ; height 0·42 mm ; width 0·32 mm. Io.6022, carapace (Pl. 1, fig. 5), length 0·82 mm ; height 0·45 mm ; width 0·37 mm.

Cytherella mandawaensis sp. nov.

Pl. 1, figs 3, 4, 7–9

Diagnosis. *Cytherella* with elongate carapace ; dorsal margin arched just behind muscle scar depression.

Holotype. Io.6023, carapace, sample B223 (Pl. 1, fig. 3).

Paratypes. Io.6024–8, samples B219 and B223.

Horizon and Locality. Middle or Upper Kimmeridgian ; samples B219 and B223, Mandawa River (Text-fig. 3.)

Discussion. As for all species of *Cytherella* the important diagnostic feature is the carapace outline. The smaller left valve is more angularly arched posterodorsally than is the larger right valve, while the central muscle scar depression is either positively developed (Pl. 1, fig. 7) or almost imperceptible (Pl. 1, fig. 3). *Cytherella mandawaensis* sp. nov. differs from *C. collapsa* Grekoff in lacking the median constrictions and broadly rounded ends of that species. It also differs from *C. umbilica* sp. nov. in that it does not have the deeply recessed muscle scar depression of the latter.

DIMENSIONS. Holotype, Io.6023, carapace, length 0·68 mm ; height 0·37 mm ; width 0·21 mm. Paratypes : Io.6025, left valve (Pl. 1, fig. 8), length 0·63 mm ; height 0·34 mm. Io.6026, right valve (Pl. 1, fig. 7), length 0·68 mm ; height 0·39 mm. Io.6027, right valve (Pl. 1, fig. 4), length 0·70 mm ; height 0·41 mm. Io.6028, carapace (Pl. 1, fig. 9), length 0·68 mm ; height 0·37 mm ; width 0·24 mm.

Cytherella masuguluensis sp. nov.

Pl. 1, figs 2, 10

DIAGNOSIS. *Cytherella* with rectangular lateral outline.

HOLOTYPE. Io.6029, carapace, sample B66 (Pl. 1, fig. 2).

PARATYPES. Io.6030–1, samples B66 and BM94.

HORIZON AND LOCALITY. Middle Callovian, samples B66 and BM94, Wami River Area (Text-fig. 2).

DISCUSSION. *Cytherella masuguluensis* sp. nov. has a rather simple rectangular outline which lacks the dorsal and ventral concavities of *C. collapsa* Grekoff. It is also not so elongate as *C. mandawaensis* sp. nov. nor so slender in dorsal view. Indeed the dorsal outlines of *C. masuguluensis*, *C. mandawaensis* and *C. knysnaensis* reveal the wide variations existing between these three species.

DIMENSIONS. Holotype, Io.6029, carapace, length 0·72 mm ; height 0·43 mm ; width 0·30 mm. Paratype, Io.6030, carapace (Pl. 1, fig. 10), length 0·68 mm ; height 0·37 mm ; width 0·30 mm.

Cytherella umbilica sp. nov.

Pl. 1, figs 12–14

DIAGNOSIS. *Cytherella* having rounded oval carapace and deeply incised muscle scar depression.

HOLOTYPE. Io.6032, right valve, sample B67 (Pl. 1, fig. 13).

PARATYPES. Io.6033–5, sample B67.

HORIZON AND LOCALITY. Upper Oxfordian, samples B67, B68 and BM86, Wami River Area (Text-fig. 2).

DISCUSSION. *Cytherella umbilica* sp. nov. is very readily distinguished from other *Cytherella* species by its deep muscle scar depression and oval carapace outline. The preservation of the material is such that all specimens have adhering quartz grains which it is impossible to remove without damaging the shell.

DIMENSIONS. Holotype, Io.6032, right valve, length 0·53 mm ; height 0·36 mm. Paratypes : Io.6033, left valve (Pl. 1, fig. 12), length 0·65 mm ; height 0·40 mm. Io.6034, right valve (Pl. 1, fig. 14), length 0·82 mm ; height 0·43 mm.

Cytherella sp.

Pl. 1, fig. 6

MATERIAL. A single left valve, Io.6036, from sample B105b.

HORIZON AND LOCALITY. (?) Lower Tithonian, sample B105b, Mandawa Anticline (Text-fig. 3).

DISCUSSION. Although of rather striking appearance the preservation of the ostracod belonging to this uncommon species is such that the erection of a new species is undesirable.

DIMENSIONS. Io.6036, left valve, length 0·75 mm ; height 0·38 mm.

Genus ***CYTHERELLOIDEA*** Alexander 1929

Species of this genus are not commonly found in the Jurassic of Tanzania – their place appears to be taken by species of *Cytherella*.

Cytherelloidea brentonensis Dingle 1972

Pl. 2, fig. 1

1972 *Cytherelloidea brentonensis* Dingle : 290 ; pl. 16a–c.

MATERIAL. A single specimen, Io.6037, sample B97.

HORIZON AND LOCALITY. Middle Callovian, sample B97, Mandawa Anticline (Text-fig. 3).

DISCUSSION. *Cytherelloidea brentonensis* Dingle was first recorded from possible Callovian sediments of the Knysna Outlier, South Africa. Only one specimen has so far been found in the Tanzanian succession and this lacks the marginal dentition of the species. However, the ostracod is otherwise comparable and is regarded as being conspecific.

DIMENSIONS. Io.6037, carapace, length 0·55 mm ; height 0·32 mm ; width 0·13 mm.

Cytherelloidea sp.

Pl. 1, fig. 15

MATERIAL. Two specimens, Io.6038–9, samples B219 and B107a. Io.6039 figd. Pl. 1, fig. 15.

HORIZON AND LOCALITY. Lower to Middle or Upper Kimmeridgian, samples B107a and B219, Mandawa Anticline (Text-fig. 3).

DISCUSSION. A very rare species represented by two single valves and characterized by a sigmoid central rib enclosed by a peripheral ridge. The Upper Cretaceous *Cytherelloidea umzambaensis* Dingle 1969 is close to this species but instead of the median rib forming a V below the muscle scar depression, as in *Cytherelloidea* sp., the rib in *C. umzambaensis* has a much sharper right-angled bend and a straight course below the muscle scar depression.

DIMENSIONS. Io.6039, left valve, length 0·65 mm ; height 0·34 mm.

Suborder PODOCOPINA Sars 1866
Superfamily **BAIRDIACEA** Sars 1888
Family **BAIRDIIDAE** Sars 1888
Genus ***BAIRDIA*** McCoy 1844

Representatives of the genus *Bairdia* are only rarely found in the Jurassic sediments examined, possibly owing to an unfavourable environment. Precise reasons for this are, however, at present uncertain.

Bairdia sp. A

Pl. 2, fig. 14

MATERIAL. A single specimen, Io.6040, sample B223.

HORIZON AND LOCALITY. Middle or Upper Kimmeridgian, samples B219 and B223, Mandawa Anticline (Text-fig. 3).

DISCUSSION. Of the two juvenile specimens found of this species only the figured specimen has a terminal posterior spine on each valve. The absence of adult specimens presents a situation often encountered in the Lower Jurassic of England. No precise reasons for this are known but it may indicate that the species did not live in that particular area and only juvenile instars were brought in by current action.

DIMENSIONS. Io.6040, carapace, length 0·29 mm ; height 0·18 mm ; width 0·14 mm.

Bairdia sp. B

Text-fig. 4 (overleaf)

MATERIAL. A single specimen, Io.6041, sample B68.

HORIZON AND LOCALITY. Upper Oxfordian, samples B2 and B68, Wami River Area (Text-fig. 2).

DISCUSSION. Only a single adult specimen, a broken right valve, has been found of this species although a number of small juvenile instars are considered to be conspecific. The figured specimen (Io.6041) has rather large, shallow pits ornamenting the central part of the valve but there is insufficient material available to name the species.

Bairdia sp. C

Pl. 2, figs 9, 13

MATERIAL. Two specimens, Io.6042–3, samples B97 and B114 respectively.

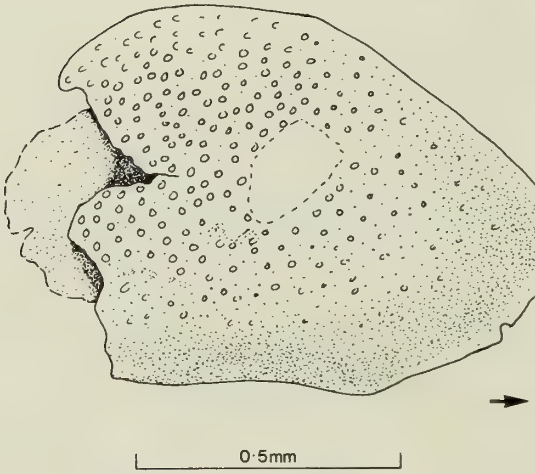

FIG. 4. *Bairdia* sp. B. Broken right valve, Io.6041.

HORIZON AND LOCALITY. Middle Callovian, samples B97 and B114, Wami River Area (Text-fig. 2).

DISCUSSION. Two complete specimens and a number of fragmentary specimens have been obtained. The single juvenile instar (Io.6043) may not be conspecific but is retained here for the present. Adult specimens do not possess the surface pitting of *Bairdia* sp. B and are further contrasted by the presence of upturned anterior and posterior ends.

DIMENSIONS. Io.6042, carapace (Pl. 2, fig. 13), length 0·82 mm ; height 0·46 mm ; width 0·34 mm. Io.6043, juvenile carapace (Pl. 2, fig. 9), length 0·50 mm ; height 0·29 mm ; width 0·21 mm.

Genus ***BYTHOCYPRIS*** Brady 1880

The genus *Bythocypris* has not previously been recognized from the Mesozoic sediments of the Indian Ocean region. Although very rare, two distinct species are recognized here but left under open nomenclature.

Bythocypris sp. A

Pl. 2, fig. 8

MATERIAL. A single specimen, Io.6044, sample B219.

HORIZON AND LOCALITY. Middle or Upper Kimmeridgian, sample B219, Mandawa Anticline (Text-fig. 3).

DISCUSSION. A single left valve characterized by having an elongate carapace with almost straight ventral margin and arched dorsal margin having distinct cardinal angles.

DIMENSIONS. Io.6044, left valve, length 0·74 mm ; height 0·39 mm.

Bythocypris sp. B

Pl. 2, fig. 7 ; Text-fig. 5a, b

MATERIAL. Two specimens, Io.6045–6, samples B67 and B68 respectively.

HORIZON AND LOCALITY. Upper Oxfordian, samples BM86, B67 and B68, Wami River Area (Text-fig. 2).

DISCUSSION. A rare ostracod present in three of the Oxfordian samples. *Bythocypris* sp. B differs from sp. A in being more squat in outline with well-rounded terminal margins. The ventral margin being incurved medially differs from the almost straight ventral margin of sp. A ; the dorsal margin also differs in lacking the acute posterior cardinal angle and as a result is more uniformly arched.

DIMENSIONS. Io.6045, carapace (Pl. 2, fig. 7), length 0·70 mm ; height 0·36 mm ; width 0·28 mm. Io.6046, carapace (Text-fig. 5), length 0·71 mm ; height 0·43 mm ; width 0·31 mm.

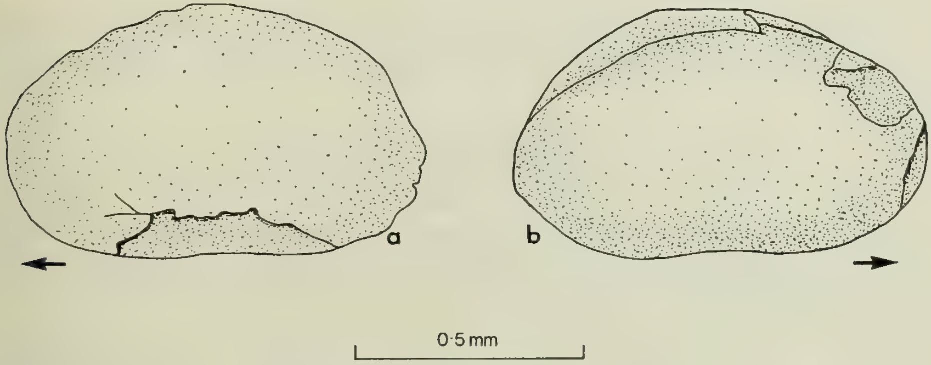

FIG. 5a, b. *Bythocypris* sp. B. Left and right views, carapace Io.6046.

Superfamily **CYPRIDACEA** Baird 1845

Family **PARACYPRIDIDAE** Sars 1923

Genus ***PARACYPRIS*** Sars 1866

Paracypris aff. ***P. contermia*** Ljubimova & Mohan 1960

Pl. 2, fig. 6

MATERIAL. A single specimen, Io.6047, sample B66.

HORIZON AND LOCALITY. Middle Callovian, sample B66, Wami River Area (Text-fig. 2).

DISCUSSION. A very rare ostracod rather more elongate in outline than the *Paracypris contermia* described by Ljubimova & Mohan from the Callovian of Kutch, but which nevertheless has a close affinity with that species. If additional material had been available possibly the Tanzanian material could have been recognized as conspecific.

Dimensions. Io.6047, carapace, length 0·55 mm ; height 0·24 mm ; width 0·17 mm.

Paracypris sp. A

Pl. 2, figs 4, 5

Material. Two specimens, Io.6048–9, sample B223.

Horizon and Locality. Middle or Upper Kimmeridgian, samples B219 and B223, Mandawa Anticline (Text-fig. 3).

Discussion. *Paracypris* sp. A is a rare ostracod too poorly preserved to identify specifically. It is, however, close to *P.* cf. *acris* Oertli of Grekoff 1963 although it is not so elongate and has a more oblique antero-dorsal slope in the right valve. The two forms are specifically distinct but both belong to that group of *Paracypris* species having a very sharply pointed posterior end and a line of greatest length extending along the ventral margin.

Dimensions. Io.6048, carapace (Pl. 2, fig. 5), length 0·72 mm ; height 0·35 mm ; width 0·26 mm. Io.6049, carapace (Pl. 2, fig. 4), length 0·77 mm ; height 0·33 mm ; width 0·28 mm.

Paracypris sp. B

Pl. 2, fig. 2

Material. A single specimen, Io.6050, sample BM94.

Horizon and Locality. Middle Callovian to Upper Oxfordian, samples BM94 and B2, Wami River Area (Text-fig. 2).

Discussion. Smaller than *Paracypris* sp. A and with a much longer antero-dorsal slope, the line of greatest height being further back and almost median in position. As the illustrations show, there is no difficulty in distinguishing between these two species and here again there is insufficient material to identify the species specifically.

Dimensions. Io.6050, carapace, length 0·54 mm ; height 0·22 mm ; width 0·13 mm.

Genus ***PONTOCYPRELLA*** Ljubimova 1955

Pontocyprella sp.

Pl. 2, figs 15–17

Material. Five registered specimens, Io.6051–5, sample B223, of which Io.6052 and 6055 are not here figured.

Horizon and Locality. Middle or Upper Kimmeridgian, samples B219 and B223, Mandawa Anticline (Text-fig. 3).

Discussion. A total of eight juvenile instars and a single adult carapace are retained here under open nomenclature. This species differs from the Callovian

Pontocyprella sp. of Grekoff 1963 in having a much straighter ventral margin along which the line of greatest length is situated. The dorsal margin is also less strongly arched in the present material.

Dimensions. Io.6051, left valve (Pl. 2, fig. 16), length 0·43 mm; height 0·20 mm. Io.6053, carapace (Pl. 2, fig. 17), length 0·41 mm ; height 0·20 mm ; width 0·16 mm. Io.6054, right valve (Pl. 2, fig. 15), length 0·35 mm ; height 0·17 mm. Io.6055, adult carapace, length 0·56 mm ; height 0·26 mm ; width 0·24 mm.

Superfamily **DARWINULACEA** Brady & Norman 1889

Family **DARWINULIDAE** Brady & Norman 1889

Genus ***DARWINULA*** Brady & Robertson 1885

Darwinula sp.

Pl. 2, fig. 12

Material. A single specimen, Io.6056, sample B114.

Horizon and Locality. Middle Callovian, sample B114, Mandawa Anticline (Text-fig. 3).

Discussion. A single carapace in a rather poor state of preservation but distinguishable from the Middle Jurassic *Darwinula* sp. of Grekoff 1963 by its long elongate carapace, lacking the curved dorsal and ventral margins of the latter. The presence of *Darwinula*, together with charophytes, in an otherwise marine environment, indicates a near-shore environment subject to some freshwater influence.

Dimensions. Io.6056, carapace, length 0·85 mm ; height 0·37 mm ; width 0·31 mm.

Superfamily **CYTHERACEA** Baird 1850

Family **BYTHOCYTHERIDAE** Sars 1926

Genus ***MONOCERATINA*** Roth 1928

Monoceratina sp. A

Pl. 2, figs 10, 11

Material. Two specimens, Io.6057–8, sample B219.

Horizon and Locality. Middle or Upper Kimmeridgian, samples B219 and B223, Mandawa Anticline (Text-fig. 3).

Discussion. A rare species having some feature in common with the Portlandian/Valanginian *Monoceratina* 129 of Grekoff 1963 from Madagascar, but differing in lacking the coarse surface pitting of that species. *Monoceratina* sp. A would appear to be new and, so far, known only from the Middle or Upper Kimmeridgian.

Dimensions. Io.6057, carapace (Pl. 2, fig. 10), length 0·71 mm ; height 0·43 mm ; width 0·35 mm. Io.6058, carapace (Pl. 2, fig. 11), length 0·71 mm ; height 0·39 mm ; width 0·28 mm.

Monoceratina sp. B

Pl. 2, fig. 3

Material. A single specimen, Io.6059, sample B97.

Horizon and Locality. Middle Callovian, sample B97, Mandawa Anticline (Text-fig. 3).

Discussion. A strongly sulcate, highly ornamented species of *Monoceratina* for which there is no comparable form from the Indian Ocean region. The nearest species is *M. scrobiculata* Triebel & Bartenstein 1938 from the Lower Jurassic of Europe but this differs by having the coarse pitting covering the entire surface of the valve rather than being restricted to the central part as in *M.* sp. B. *M. scrobiculata* also differs in having the line of greatest length situated higher up on the valve, passing along the dorsal margin rather than through the mid-point as in *M.* sp. B.

Dimensions. Io.6059, left valve, length 0·49 mm ; height 0·24 mm.

Family **PROGONOCYTHERIDAE** Sylvester-Bradley 1948

Subfamily **PROGONOCYTHERINAE** Sylvester-Bradley 1948

The genera placed in this subfamily are all related on carapace outline, which is subquadrate to subrectangular with rounded anterior and triangular posterior ends and with the ventro-lateral part of the valve tending to overhang the venter. Internally the duplicature is of medium width without a vestibule. Marginal pore canals are simple, generally straight but may be slightly curved and relatively few in number. Normal pore canals are of simple type although sieve plates are known in some genera. Muscle scars consist of a subvertical row of four oval adductor scars with a rounded or slightly crescentic antero-dorsal frontal scar and a rounded antero-ventral mandibular scar. Hinge types are variable, ranging from lophodont to entomodont.

Genus ***MAJUNGAELLA*** Grekoff 1963

The genus *Majungaella* was first described by Grekoff from the Upper Jurassic and Lower Cretaceous of Madagascar ; the type species, *M. perforata* Grekoff, ranges from the Kimmeridgian to the Portlandian. Grekoff (1963) also described a second species from Madagascar, *M. nematis*, which has a range of Portlandian to Valanginian. Subsequently species of *Majungaella* have been described from the Mesozoic of India (Guha 1975?), East Africa (Bate 1969), South Africa (Dingle 1971, 1972) and from Australia (Bate 1972).

Dingle (1972) considered *Majungaella* to be a subgenus of the almost exclusively northern hemisphere genus *Progonocythere* Sylvester-Bradley 1948. *Progonocythere* sensu stricto is certainly very close to *Majungaella* in that it has a comparable carapace outline and the same type of hinge and muscle scar arrangement. The details of the duplicature also agree, although the marginal pore canals differ slightly in number and shape. *Progonocythere* has 6–10 straight anterior marginal canals whereas in *Majungaella* the canals are slightly curved and increase in number from

14–20 in the Jurassic to 28–30 in the Cretaceous. *Majungaella* may be further differentiated by its surface sculpture of pits often concentrically arranged. Because of these differences, consistent for all species, the two are retained here as distinct genera.

Progonocythere has a stratigraphical range restricted to the Jurassic and a geographical range virtually restricted to the region north of the Tethys. South of the Tethys, the southern genus *Majungaella* appears in the Middle Jurassic and ranges through into the Upper Cretaceous.

Recently, Krömmelbein (1975) has removed from *Majungaella* those Upper Cretaceous species having an increased number of anterior marginal pore canals and a distinctly angled but narrow posterior end. These forms he has placed in the new genus *Tickalaracythere*. Rossi de Garcia (1972) has described *Novocythere*, an Upper Cretaceous genus from Argentina, which from the illustrations appears to be synonymous with *Tickalaracythere*. Krömmelbein (personal communication) informs me that Rossi de Garcia has written to him stating that the hinge of *Novocythere* is not the same and that the expanded portion of the median element is to the rear of the hinge. This is not correct according to the illustrations of Rossi de Garcia. There is, therefore, some taxonomic confusion which can only be cleared up by examining Rossi de Garcia's material from Argentina and by comparing it with material from Australia placed by Krömmelbein in *Tickalaracythere*. It is not my intention here to revise the genus *Majungaella*, but on present evidence I would prefer to retain *Tickalaracythere* or *Novocythere*, or both, as subgenera of *Majungaella*.

Majungaella perforata Grekoff 1963

Pl. 3, figs 1–3, 7

1963 *Majungaella perforata* Grekoff : 1743 ; pl. 5, figs 134–140 ; pl. 9, figs 230, 233.

MATERIAL. Six specimens, Io.6060–5, samples B105b, B110 and B111.

HORIZON AND LOCALITY. (?) Lower to Upper Tithonian, samples B105b, B110 and B111, Mandawa Anticline (Text-fig. 3).

DISCUSSION. Grekoff (1963) records *M. perforata* from the Kimmeridgian and Portlandian of Madagascar while Guha (1975?) records it from the Callovian to Kimmeridgian of Kutch. This last recorded range would appear to be excessive as the present investigation shows species of *Majungaella* to be more restricted than this. In Tanzania *M. perforata* has been found in the (?) Lower and Upper Tithonian but below this it is replaced by the Middle or Upper Kimmeridgian *M. praeperforata* sp. nov., a closely related and similar species. The Tithonian interval has suffered considerable decalcification and as a result good specimens of *M. perforata* are rare.

DIMENSIONS. Io.6062, female carapace (Pl. 3, fig. 7), length 0·73 mm ; height 0·49 mm ; width 0·43 mm. Io.6063, male carapace (Pl. 3, fig. 3), length 0·78 mm ; height 0·49 mm ; width 0·44 mm. Io.6064, female carapace (Pl. 3, fig. 2), length 0·74 mm ; height 0·49 mm ; width 0·40 mm. Io.6065, male carapace (Pl. 3, fig. 1), length 0·84 mm ; height 0·56 mm ; width 0·47 mm.

Majungaella praeperforata sp. nov.

Pl. 3, figs 4–6, 8–10; Pl. 4, figs 1–3; Text-fig. 6

DIAGNOSIS. Large species of *Majungaella*: male dimorphs 0·84–0·95 mm, female dimorphs 0·80–0·85 mm in length. Lateral surface coarsely ornamented by large pits forming rows extending down from the dorsal margin, diverging initially but turning inwards ventro-laterally.

HOLOTYPE. Io.6066, female carapace, sample B219 (Pl. 3, fig. 6).

PARATYPES. Io.6067–74, sample B219.

HORIZON AND LOCALITY. Middle or Upper Kimmeridgian, samples B219, B222 and B223, Mandawa Anticline (Text-fig. 3).

DESCRIPTION. **Carapace** dimorphic, thick-shelled and robust; strongly convex in dorsal and ventral views. Ornamentation consisting of large pits forming rows diverging away from the dorsal margin but turning inwards ventro-laterally. Ventral surface with two distinct ridges on each valve. Left valve larger than right. **Hinge** entomodont, strongly developed. **Muscle scars** consisting of four rounded adductor scars with a large, rounded antero-dorsal frontal scar and an oval antero-ventral mandibular scar (Text-fig. 6; Pl. 3, fig. 9). **Duplicature** (calcified inner lamella) of moderate width with 18–19 straight to slightly curved anterior **marginal pore canals** (Pl. 3, fig. 10). Inner margin and line of concrescence coincide.

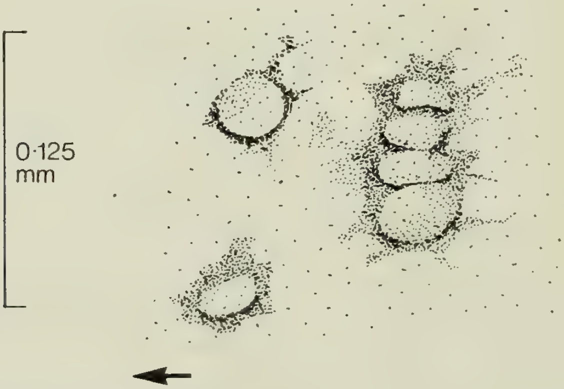

FIG. 6. *Majungaella praeperforata* sp. nov. Muscle scars, female right valve, paratype Io.6070.

DIMENSIONS. Holotype, Io.6066, female carapace (Pl. 3, fig. 6), length 0·85 mm; height 0·60 mm; width 0·53 mm. Paratypes: Io.6067, female left valve (Pl. 3, fig. 4), length 0·81 mm; height 0·57 mm. Io.6068, male left valve (Pl. 3, fig. 5), length 0·95 mm; height 0·61 mm. Io.6069, male right valve (Pl. 3, fig. 10), length 0·84 mm; height 0·45 mm. Io.6070, female right valve (Pl. 3, fig. 9; Text-fig. 6), length 0·80 mm; height 0·53 mm. Io.6071, female carapace (Pl. 4, fig. 2), length

0·85 mm ; height 0·60 mm ; width 0·54 mm. Io.6072, female left valve (Pl. 3, fig. 8), length 0·78 mm ; height 0·66 mm. Io.6073, male right valve (Pl. 4, fig. 1), length 0·95 mm ; height 0·55 mm. Io.6074, female carapace (Pl. 4, fig. 3), length 0·60 mm ; height 0·52 mm.

Discussion. *Majungaella praeperforata* sp. nov. closely resembles the Upper Kimmeridgian *M. perforata* Grekoff but differs in size (*M. perforata* from Madagascar, length 0·69–0·80 mm ; from Tanzania, length female 0·74–0·78 mm, male 0·84 mm), the females ranging from 0·80 to 0·85 mm and the males up to 0·95 mm. *M. praeperforata* is also more robust in dorsal view, being very much more rotund in outline (cf. Pl. 3, fig. 7 and Pl. 4, figs 2, 3). There is also a slight difference in ornamentation between these two species : in *M. praeperforata* the pits are arranged in rows initially diverging from the dorsal margin whereas in *M. perforata* this development of rows does not exist in the dorsal and dorso-median region, the pits being more haphazard in their arrangement. In both there is a tendency to form rows in the ventro-lateral region.

M. praeperforata sp. nov. and *M. perforata* Grekoff possess a strongly pitted shell surface that differs from the ornamentation pattern of ridges and pits present in the younger *M. nematis* Grekoff 1963.

Majungaella kimmeridgiana sp. nov.

Pl. 4, figs 4–11 ; Pl. 5, figs 1–3 ; Text-fig. 7a–c

Diagnosis. *Majungaella* with subtrigonal lateral outline in female dimorph ; male subrectangular. Males 0·75–0·77 mm, females 0·64–0·69 mm in length. Shell surface coarsely pitted : pits arranged either in rows extending down from dorsal margin or irregularly spaced over carapace.

Holotype. Io.6075, female carapace, sample B103a (Pl. 4, fig. 4).

Paratypes. Io.6076–86, samples B103a and B104a.

Horizon and Locality. Lower Kimmeridgian, samples B103a, B104a and B106a, Mandawa Anticline (Text-fig. 3).

Description. **Carapace** dimorphic with left valve larger than the right, outline of shell as illustrated. Ornamentation as illustrated : ventral ribbing not well developed in anterior part of carapace. **Hinge** entomodont, robust and well developed. **Muscle scars** an oblique row of four, oval to rounded, with a rounded antero-dorsal frontal scar and a rounded antero-ventral mandibular scar (Text-fig. 7c). **Duplicature** broad ; inner margin and line of concrescence coinciding. **Marginal pore canals** slightly curved ; anteriorly 15–19 in number (one branching in Text-fig. 7b) and with the curve of the canals exaggerated by the internal convexity of the valve. Posteriorly there are five marginal canals some having a bulbous development at their mid-length.

Dimensions. Holotype, Io.6075, female carapace (Pl. 4, fig. 4), length 0·68 mm ; height 0·48 mm ; width 0·43 mm. Paratypes : Io.6076, male carapace (Pl. 5, fig. 1), length 0·77 mm ; height 0·47 mm ; width 0·47 mm. Io.6077, female left

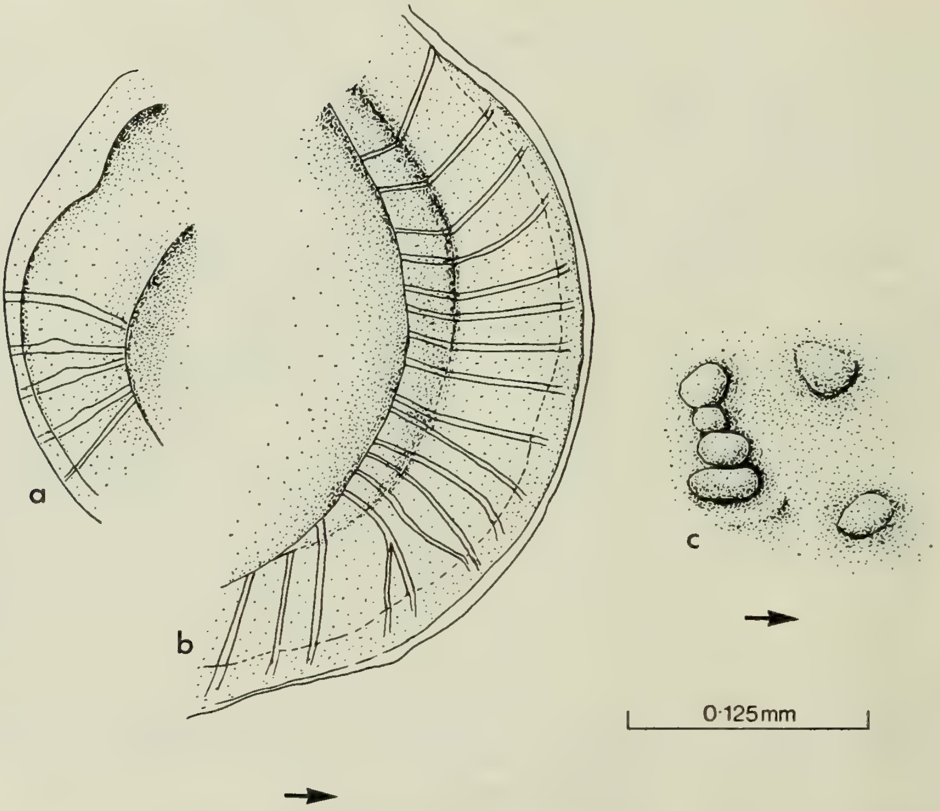

FIG. 7a–c. *Majungaella kimmeridgiana* sp. nov. a, b. Posterior and anterior marginal pore canals, female left valve, paratype Io.6087. c. Muscle scars, female left valve, paratype Io.6079.

valve (Pl. 4, fig. 9), length 0·69 mm ; height 0·47 mm. Io.6078, female right valve (Pl. 4, fig. 11), length 0·65 mm ; height 0·43 mm. Io.6080, female left valve (Pl. 4, fig. 8), length 0·68 mm ; height 0·47 mm. Io.6081, male carapace (Pl. 4, fig. 7), length 0·77 mm ; height 0·49 mm ; width 0·45 mm. Io.6082, male carapace (Pl. 5, fig. 3), length 0·76 mm ; height 0·47 mm ; width 0·43 mm. Io.6083, male left valve (Pl. 5, fig. 2), length 0·75 mm ; height 0·47 mm. Io.6084, female carapace (Pl. 4, fig. 6), length 0·66 mm ; height 0·47 mm ; width 0·42 mm. Io.6085, female carapace (Pl. 4, fig. 5), length 0·64 mm ; height 0·44 mm ; width 0·41 mm. Io.6086, female carapace (Pl. 4, fig. 10), length 0·69 mm ; height 0·47 mm ; width 0·43 mm.

DISCUSSION. *Majungaella kimmeridgiana* sp. nov. is smaller than *M. praeperforata* sp. nov. and *M. perforata* Grekoff and, in the female, rather more subtrigonal in outline. The ornamentation is closely comparable in some individuals but differs markedly in those where the pits are not arranged in rows (Pl. 4, fig. 5 and

Pl. 5, fig. 2). The ventral ribbing of *M. kimmeridgiana* is less distinctly developed than in *M. praeperforata* and the marginal pore canals are more distinctly curved.

Majungaella oxfordiana sp. nov.

Pl. 5, figs 4–9

DIAGNOSIS. *Majungaella* with weak surface ornamentation of pits. Carapace distinctly tapered to narrow posterior end.

HOLOTYPE. Io.6088, female carapace, sample B2 (Pl. 5, fig. 5).

PARATYPES. Io.6089–94, sample B2.

HORIZON AND LOCALITY. Upper Oxfordian, samples B2 and B67, Wami River Area (Text-fig. 2).

DESCRIPTION. **Carapace** with strong posterior taper, dimorphic ; males very elongate with a more marked posterior taper than in the females. Left valve larger than the right. Ornamentation weak ; pits appear to be irregularly scattered over the shell surface although linearly arranged in the ventro-lateral region. **Hinge** entomodont, robust. **Muscle** scars not seen. **Duplicature** of moderate width with approximately 16 slightly curved anterior marginal pore canals.

DIMENSIONS. Holotype, Io.6088, female carapace (Pl. 5, fig. 5), length 0·72 mm ; height 0·51 mm ; width 0·43 mm. Paratypes : Io.6089, male carapace (Pl. 5, fig. 4), length 0·77 mm ; height 0·44 mm ; width 0·38 mm. Io.6090, female left valve (Pl. 5, fig. 8), length 0·68 mm ; height 0·46 mm. Io.6091, female right valve (Pl. 5, fig. 9), length 0·70 mm ; height 0·44 mm. Io.6092, female left valve (Pl. 5, fig. 7), length 0·72 mm ; height 0·48 mm. Io.6093, female carapace (Pl. 5, fig. 6), length 0·69 mm ; height 0·47 mm ; width 0·40 mm.

DISCUSSION. *Majungaella oxfordiana* sp. nov. is the same size as *M. kimmeridgiana* sp. nov. but is not so positively ornamented and differs in carapace outline. The extremely strong posterior taper present in the male of *M. oxfordiana* makes it almost identical to the male of *Progonocythere laeviscula* Ljubimova & Mohan 1960, although it lacks the diagnostic crescent-shaped median sulcus of the latter.

The material available of *M. oxfordiana* is very poorly preserved and tends to be encrusted by quartz grains. As a result the determination of the surface ornamentation is not always possible and many specimens appear to be smooth.

Majungaella mundula (Grekoff)

Pl. 5, figs 10–13

1963 *Progonocythere mundula* Grekoff : 1738, pl. 4, figs 92–95.

MATERIAL. Seven specimens, Io.6095–101, samples B66 and B97.

HORIZON AND LOCALITY. Middle Callovian, sample B66, Wami River Area (Text-fig. 2) and sample B97, Mandawa Anticline (Text-fig. 3).

DISCUSSION. Grekoff (1963) described a new ostracod of the genus *Progonocythere* from the Middle Callovian of Madagascar. This species, *P. mundula*, is small (length 0·43–0·50 mm), has a strongly pitted shell surface and apparently lacks sexual dimorphism. Guha (1975?) records this species from the Bathonian/Callovian interval of Kutch and it is recorded here from the Middle Callovian of Tanzania. The Tanzanian specimens are slightly larger than those recorded from Madagascar and have a length of 0·53–0·55 mm. No measurements are available for the Indian material.

Of the species from Madagascar assigned to *Progonocythere* by Grekoff, only *Progonocythere laeviscula* Ljubimova & Mohan 1960 is considered truly to represent that genus south of the Tethys. *P. mundula* is considered to belong more correctly to the genus *Majungaella* of which it is currently the oldest known species.

Dimensions. Io.6095, carapace (Pl. 5, fig. 12), length 0·49 mm ; height 0·35 mm ; width 0·29 mm. Io.6096, carapace (Pl. 5, fig. 10), length 0·49 mm ; height 0·36 mm ; width 0·30 mm. Io.6097, carapace (Pl. 5, fig. 13), length 0·55 mm ; height 0·39 mm ; width 0·32 mm. Io.6098, carapace (Pl. 5, fig. 11), length 0·53 mm ; height 0·37 mm ; width 0·37 mm.

Genus ***FASTIGATOCYTHERE*** Wienholz 1967

Fastigatocythere is retained here as a distinct genus despite the fact that Dépêche (1973) relegated it to the position of a subgenus of *Lophocythere*, almost certainly because Wienholz included *Lophocythere interrupta* Triebel 1951 in *Fastigatocythere*. However, the type species of *Fastigatocythere*, *F. rugosa* Wienholz 1967, does not appear to be congeneric with *L. interrupta* and the two species are considered to belong to separate genera.

In addition to *F. rugosa* and *Progonocythere juglandica* (Jones 1884), Wienholz included the following Madagascar species of Grekoff 1963 in her genus : *Progonocythere accesa*, *P. bicruciata*, *P. befotakaensis*, *P.* 2392 and the subspecies *P. juglandica malgachica*. This effectively removed the majority of the southern species assigned to *Progonocythere* from that genus ; of the remainder only *Progonocythere laeviscula* Ljubimova & Mohan is considered to represent *Progonocythere* satisfactorily south of the Tethys.

Fastigatocythere aff. ***brentonensis*** (Dingle 1972)

Pl. 6, figs 9, 10 ; Pl. 7, fig. 9

Material. Three specimens, Io.6102–4, sample B223.

Horizon and Locality. Middle or Upper Kimmeridgian, samples B219 and B223, Mandawa Anticline (Text-fig. 3).

Discussion. Of the three left valves assigned to this species only one (Io.6102) possesses obliquely transverse ridges and thus more closely resembles *F. brentonensis* (Dingle), but it is less positively ornamented, lacking the surface reticulation illustrated by Dingle. All three specimens are smaller than Dingle's material and could represent juvenile instars. In the absence of further material it is not possible to do more than draw attention to its affinities with the South African ostracod.

DIMENSIONS. Io.6102, left valve (Pl. 6, fig. 9), length 0·43 mm ; height 0·26 mm. Io.6104, left valve (Pl. 6, fig. 10), length 0·37 mm ; height 0·22 mm.

Genus *TRICHORDIS* Grekoff 1963

Trichordis triangula sp. nov.

Pl. 6, figs 1–8, 14 ; Text-fig. 8a, b

DIAGNOSIS. Species of *Trichordis* with distinct posterior taper and triangular lateral outline. Three prominent lateral ribs ; ventral surface deeply pitted with three ridges on each valve.

HOLOTYPE. Io.6105, female carapace, sample B219 (Pl. 6, figs 1, 5).

PARATYPES. Io.6106–12 ; samples B107a, B219 and BM86.

HORIZON AND LOCALITY. Upper Oxfordian ; samples BM86 and B68, Wami River Area (Text-fig. 2) and Lower and Middle or Upper Kimmeridgian ; samples B107a, B219 and B223, Mandawa Anticline (Text-fig. 3).

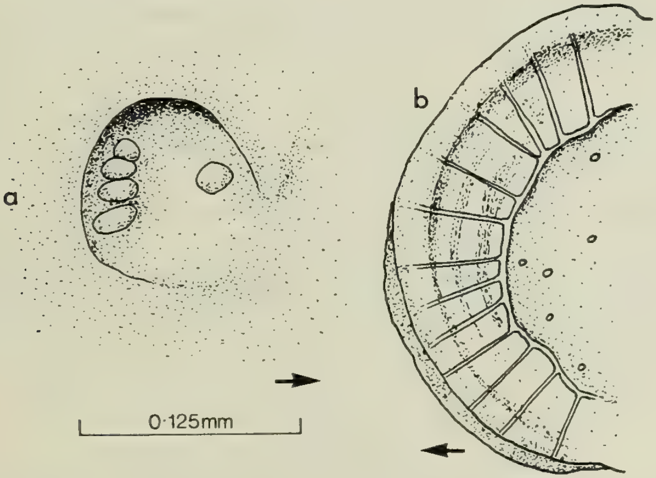

FIG. 8a, b. *Trichordis triangula* sp. nov. a. Muscle scars, female left valve, paratype Io.6110. b. Anterior marginal pore canals, male right valve, paratype Io.6112.

DESCRIPTION. **Carapace** dimorphic although the presumed males are only slightly more elongate than the females. Left valve larger than the right. Ornamentation rather insignificant, consisting of weak pits superimposed upon the structural ribs. **Hinge** entomodont, rather strongly developed. **Duplicature** broad anteriorly and, apart from a narrow anterior zone into which run the 12–14 straight **marginal pore canals** (Text-fig. 8b), the inner margin coincides with the line of concrescence. **Selvage** prominent, anterior **flange** distinct. **Muscle scars** consist of four oval adductor scars and a rounded frontal scar (Text-fig. 8a) internally set in a deep muscle scar pit, reflected on the outside of the valve by a broad swelling.

DIMENSIONS. Holotype, Io.6105, female carapace (Pl. 6, figs 1, 5), length 0·50 mm ; height 0·32 mm ; width 0·26 mm. Paratypes : Io.6106, female left valve (Pl. 6, fig. 7), length 0·43 mm ; height 0·29 mm. Io.6107, male left valve (Pl. 6, fig. 4), length 0·42 mm ; height 0·23 mm. Io.6108, female carapace (Pl. 6, fig. 6), length 0·51 mm ; height 0·31 mm ; width 0·26 mm. Io.6109, female left valve (Pl. 6, fig. 3), length 0·49 mm ; height 0·32 mm. Io.6110, female left valve (Pl. 6, fig. 8 ; Text-fig. 8a), length 0·51 mm ; height 0·33 mm. Io.6111, male right valve (Pl. 6, fig. 14), length 0·50 mm ; height 0·27 mm.

DISCUSSION. *Trichordis triangula* sp. nov. differs from *T. praetexta* Grekoff 1963 in having the three lateral ridges of the genus more prominently developed and having a more triangular outline in lateral view. The hinge of *T. triangula* is entomodont and thus differs from the modified entomodont hinge of *T. praetexta* in which the median element, apart from the two antero-median teeth, appears to be smooth. There is also an increased number of anterior marginal pore canals which, being straight and simple, lack the median swelling of those present in *T. praetexta*. Despite all the differences that go beyond ordinary specific characters it is considered that this Tanzanian species belongs to *Trichordis*, although it may be necessary later to subdivide the genus.

Genus ***MANDELSTAMIA*** Ljubimova 1955

The genus *Mandelstamia* was placed in the family Cytheridae by Orlov (1960), whereas Moore (1961) grouped it with others under an uncertain family heading. Here *Mandelstamia* is considered to belong in the Progonocytherinae, having in common with the other genera grouped here the general carapace outline, straight or only slightly curved rather simple marginal pore canals and muscle scar pattern.

Mandelstamia grekoffi sp. nov.

Pl. 7, figs 1–6

DIAGNOSIS. *Mandelstamia* with subrectangular carapace tapering to narrowly rounded posterior end. Shell surface with neat reticulate ornamentation.

HOLOTYPE. Io.6172, right valve, sample B219 (Pl. 7, fig. 4).

PARATYPES. Io.6168–71, samples B219 and B223.

HORIZON AND LOCALITY. Middle or Upper Kimmeridgian, samples B219 and B223, Mandawa Anticline (Text-fig. 3).

DESCRIPTION. **Carapace** outline and ornamentation as illustrated. Shallow median constriction of carapace visible in dorsal view. Ventro-lateral surface convex, partially overhanging ventral surface. **Hinge** lophodont. **Muscle scars** not observed. **Duplicature** very narrow, marginal pore canals not observed.

Dimensions. Holotype, Io.6172, right valve (Pl. 7, fig. 4), length 0·50 mm, height 0·26 mm. arpes : PatyIo.6168, left valve (Pl. 7, fig. 3), length 0·46 mm, height 0·25 mm. Io.6169, carapace (Pl. 7, fig. 2), length 0·57 mm ; height 0·30 mm ; width 0·23 mm. Io.6170, right valve (Pl. 7, figs 5, 6), length 0·64 mm ; height 0·30 mm. Io.6171, carapace (Pl. 7, fig. 1), length 0·42 mm ; height 0·21 mm ; width 0·16 mm.

Discussion. In lateral view *Mandelstamia grekoffi* sp. nov. closely resembles *Mandelstamia* ? 962 of Grekoff (1963), from the Valanginian of Madagascar. The two species are more readily distinguished in dorsal view by the absence of a median constriction and a much thicker carapace in *M.* ? 962. *Mandelstamia angulata* Kilenyi 1961, from the Lower Kimmeridgian of England, is a comparable species but although showing the median constriction is much more robust in dorsal view and not so slender in lateral outline.

Mandelstamia sp.

Pl. 7, figs 7, 8

Material. Three specimens, Io.6165–7, samples B219 and B223.

Horizon and Locality. Middle or Upper Kimmeridgian, samples B219 and B223, Mandawa Anticline (Text-fig. 3).

Discussion. *Mandelstamia* sp. is a new species represented by only three specimens. It is close to *Mandelstamia* ? 962 of Grekoff (1963), but differs by being smaller and in ornament by having larger pits between which the shell surface is upraised to form low ridges. Apart from the lophodont hinge and narrow duplicature the internal details have not been observed.

Dimensions. Io.6165, right valve (Pl. 7, fig. 8), length 0·43 mm ; height 0·23 mm. Io.6166, carapace (Pl. 7, fig. 7), length 0·47 mm ; height 0·25 mm ; width 0·19 mm.

Subfamily **PLEUROCYTHERINAE** Mandelstam 1960

Genus ***PLEUROCYTHERE*** Triebel 1951

Pleurocythere tanzanensis sp. nov.

Pl. 6, figs 11–13 ; Text-fig. 9a, b

Diagnosis. *Pleurocythere* with dorsal carina fusing anteriorly with eye node, posteriorly with median and ventral carinae. Shell surface reticulate. Hinge of antimerodont/amphidont type. Marginal pore canals straight, few in number.

Holotype. Io.6137, carapace, sample B223 (Pl. 6, figs 11, 12).

Paratypes. Io.6138–9, sample B223.

Horizon and Locality. Middle or Upper Kimmeridgian, sample B223, Mandawa Anticline (Text-fig. 3).

Description. **Carapace** and ornamentation as illustrated. The **eye node** is here more clearly visible in the left valve. Left valve larger than the right. **Hinge**

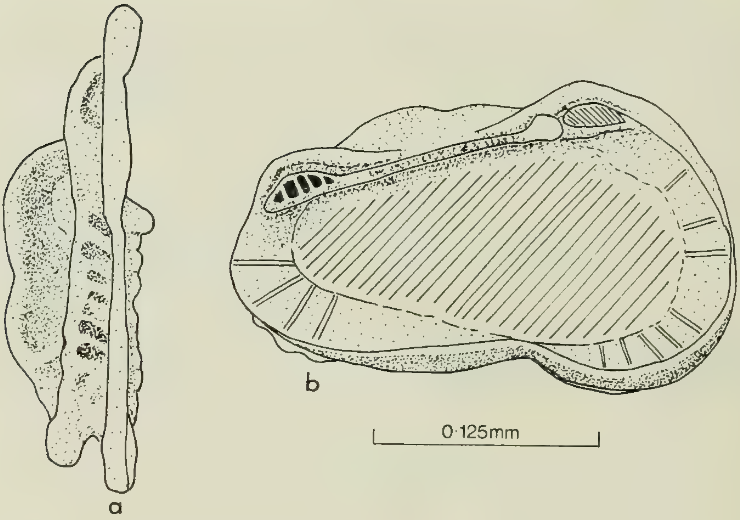

FIG. 9a, b. *Pleurocythere tanzanensis* sp. nov. Dorsal and internal views, left valve, paratype Io.6139.

of antimerodont/amphidont type, only seen in the left valve (Text-fig. 9a) where all the elements are dentate/loculate ; median element possesses a single large antero-median tooth. **Duplicature** moderately broad with few widely spaced, straight, anterior **marginal pore canals. Muscle scars** not seen.

DIMENSIONS. Holotype, Io.6137, carapace (Pl. 6, figs 11, 12), length 0·45 mm ; height 0·22 mm ; width 0·21 mm. Paratype Io.6138 (Pl. 6, fig. 13), length 0·49 mm ; height not measurable (broken).

DISCUSSION. *Pleurocythere tanzanensis* sp. nov. is placed in *Pleurocythere* on the external morphology of the carapace. There are, however, differences which set this species apart from European species. The hinge of *P. tanzanensis* differs from the normal antimerodont type in having an enlarged antero-median tooth, the hinge thereby approaching the amphidont condition. The anterior marginal pore canals are straight rather than curved as in other species and the dorsal carina fuses with the eye node. These differences are sufficient to suggest a subgeneric rank for *P. tanzanensis* but a decision on this is deferred until other southern hemisphere species have been described.

Family **SCHULERIDEIDAE** Mandelstam 1959

Genus ***AMICYTHERIDEA*** nov.

DERIVATION OF NAME. *Ami+cytheridea*, *Ami* being derived from the initial letters A.M.I. of Africa, Madagascar and India, countries in which this genus is known to occur. Gender, feminine.

DIAGNOSIS. Carapace robust, triangular in lateral outline, convex in dorsal view, dimorphic. Left valve larger than right. Sculpture of ridges arranged in triangular pattern with apex at dorsal margin. Distinct marginal borders ; oblique antero-dorsal furrow. Hinge lobodont. Duplicature broad without vestibule. Marginal pore canals anteriorly approximately 14 in number, straight but slightly curved antero-ventrally. Muscle scars a curved row of four adductors with an antero-central frontal scar.

TYPE SPECIES. *Amicytheridea ihopyensis* (Grekoff 1963).

DISCUSSION. Two species are assigned to this genus, *A. triangulata* sp. nov. from the Middle Callovian of the Mandawa Anticline (= *Procytheridea* 3330 of Grekoff (1963) from the Callovian of Madagascar), and *A. ihopyensis* (Grekoff) from the Middle Callovian of the Wami River Area, from the Bathonian/Callovian of Madagascar (Grekoff 1963) and from the Bathonian/Callovian of Kutch (Guha 1975?).

Amicytheridea is similar in ornament to the European Lower to Middle Jurassic ostracod *Ektyphocythere* Bate (1963a), but differs in having a lobodont hinge and a more positive posterior taper to the carapace. Perhaps externally more closely similar to the European Lower and Middle Jurassic ostracod *Eocytheridea* Bate (1963b), it differs internally in details of the hinge and marginal pore canals. However, *Amicytheridea* might well be shown to be phylogenetically related to *Eocytheridea*, and it is quite possible that it developed from the latter, or a common ancestor, and migrated south.

Amicytheridea ihopyensis (Grekoff 1963)

Pl. 7, figs 10–13 ; Text-fig. 10a–c

1963 *Procytheridea ihopyensis* Grekoff : 1747, pl. 6, figs 164–172, pl. 10, fig. 237.

MATERIAL. Six specimens, Io.6116–21, samples B97 and BM94.

HORIZON AND LOCALITY. Middle Callovian, sample BM94, Wami River Area (Text-fig. 2) and samples B97 and B114, Mandawa Anticline (Text-fig. 3).

DISCUSSION. Grekoff records this species from the Lower Callovian and rarely from the Upper Bathonian of Madagascar. This range is also reported by Guha from India (1975?). The total known range is therefore from the Upper Bathonian to Middle Callovian with a geographical distribution of India, East Africa and Madagascar.

Amicytheridea ihopyensis (Grekoff) is the type species of the genus and exhibits the morphological features of the family, namely a large antero-central frontal scar, anterior marginal pore canals splayed out and showing a tendency to be curved, and a rather thick-shelled, robust carapace.

DIMENSIONS. Io.6251, female carapace (Pl. 7, fig. 11), length 0·59 mm ; height 0·37 mm ; width 0·33 mm. Io.6117, female left valve (Pl. 7, fig. 10), length 0·55 mm ; height 0·35 mm. Io.6118, juvenile carapace (Pl. 7, fig. 12), length 0·44 mm ; height 0·29 mm ; width 0·29 mm. Io.6119, female carapace (Pl. 7,

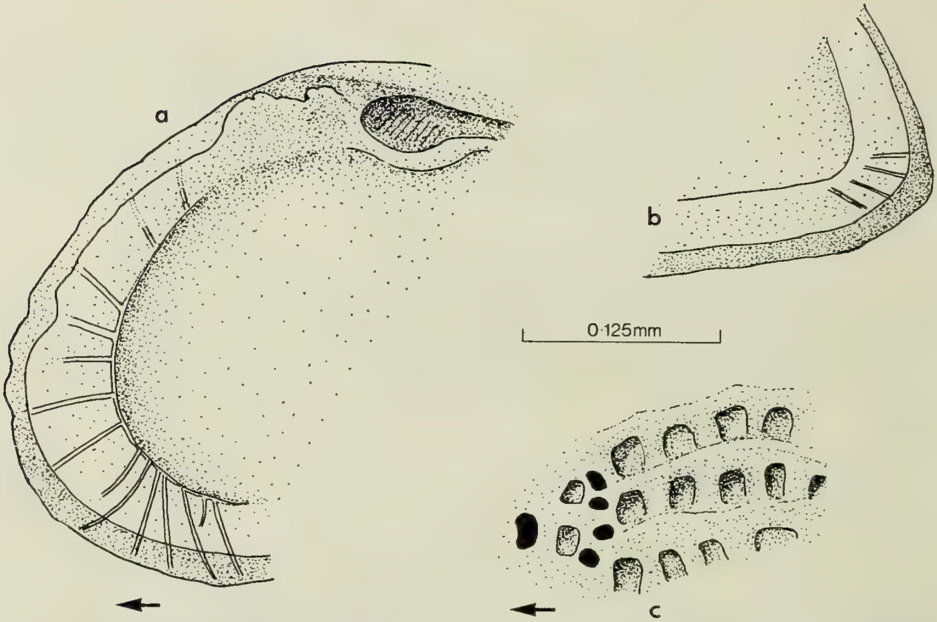

Fig. 10a–c. *Amicytheridea ihopyensis* (Grekoff). a, b. Anterior and posterior duplicature, female right valve, to show marginal pore canals, Io.6120. c. Muscle scars, male left valve exterior, Io.6121.

fig. 13), length 0·52 mm ; height 0·34 mm ; width 0·38 mm. Io.6121, male left valve (Text-fig. 10c), length 0·62 mm ; height 0·33 mm.

Amicytheridea triangulata sp. nov.

Pl. 7, figs 14–16 ; Text-fig. 11a–c

1963 *Procytheridea* ? 3330 Grekoff : 1749, pl. 6, figs 173–5.

Diagnosis. *Amicytheridea* with positive triangular ornamentation of ridges connected across interspaces by minor ridges.

Holotype. Io.6114, female left valve, sample B97 (Pl. 7, fig. 16).

Paratypes. Io.6113 and Io.6115–6, sample B97.

Horizon and Locality. Middle Callovian, sample B97, Mandawa Anticline (Text-fig. 3).

Description. **Carapace** distinctly dimorphic, males very positively tapering to posterior end. Left valve larger than right. **Ornamentation** striking – a triangular arrangement of ridges with minor connecting ridges. Anterior marginal border distinct. Oblique antero-dorsal furrow clearly marked ; postero-dorsal furrow present in female. **Hinge** lobodont, antero-median element loculate in right valve (Text-fig. 11a). **Duplicature** broad, without a vestibule. **Marginal pore canals** not clearly seen but in one specimen (Text-fig. 11b) straight, splayed out and few in number (8 observed anteriorly). **Muscle scars** not seen.

DIMENSIONS. Holotype, Io.6114, female left valve (Pl. 7, fig. 16; Text-fig. 11b, c) length 0·60 mm; height 0·37 mm. Paratypes: Io.6113, male carapace (Pl. 7, figs 14, 15), length 0·65 mm; height 0·36 mm; width 0·35 mm.

DISCUSSION. *Amicytheridea triangulata* sp. nov. is considered to be synonymous with *Procytheridea* ? 3330 described by Grekoff (1963), from the Upper Callovian of Madagascar. Although the muscle scars have not been seen and the marginal pore canals only poorly so the species is still regarded as belonging to *Amicytheridea*. The lobodont hinge of *A. triangulata* is particularly well seen in this material, which may be distinguished from *A. ihopyensis* by the more positively developed ornamentation. Indeed the carapace outline and ornamentation make *A. triangulata* closely comparable with the European Bajocian ostracod *Eocytheridea carinata* Bate 1964, although the cross ridges and lobodont hinge of *A. triangulata* serve to distinguish the two.

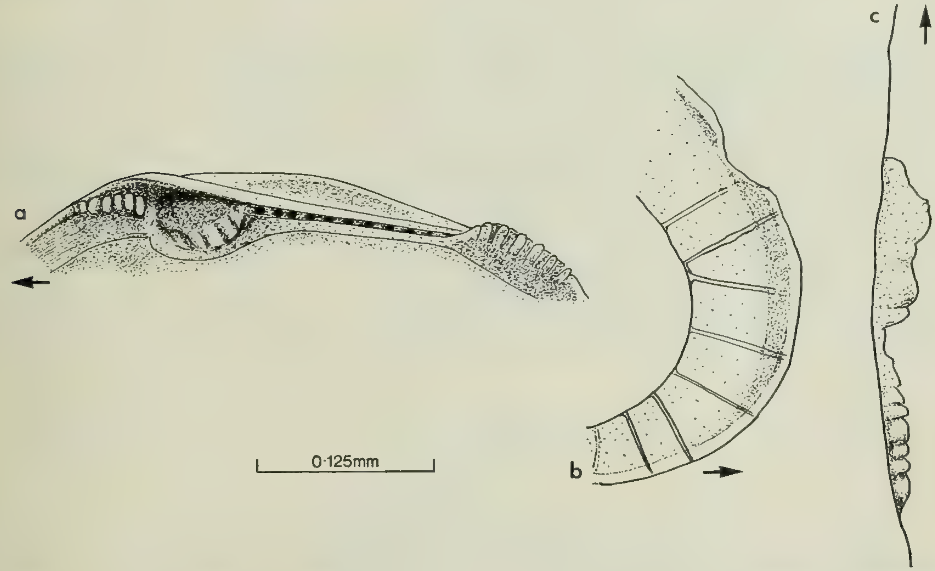

FIG. 11a–c. *Amicytheridea triangulata* sp. nov. a. Right valve hinge, female, paratype Io.6115. b, c. Anterior marginal pore canals and dorsal view of median hinge element, female left valve, holotype Io.6114.

Genus *ASCIOCYTHERE* Swain 1952

Asciocythere ? sp.

Pl. 8, figs 1, 2

MATERIAL. Two specimens, Io.6252–3, sample B114.

HORIZON AND LOCALITY. Middle Callovian, sample B114, Mandawa Anticline (Text-fig. 3).

Discussion. Two complete carapaces of a small ostracod are placed here in *Asciocythere* purely on external morphology. No internal details known.

Dimensions. Io.6252, carapace (Pl. 8, fig. 2), length 0·35 mm ; height 0·24 mm ; width 0·19 mm. Io.6253, carapace (Pl. 8, fig. 1), length 0·37 mm ; height 0·26 mm ; width 0·20 mm.

Genus ***PIRILEBERIS*** Grekoff 1963

Pirileberis prognata Grekoff 1963

Pl. 8, figs 9–11

1963 *Pirileberis prognata* Grekoff : 1750, pl. 6, figs 156–161.

Material. Nine specimens, Io.6151–7 and Io.6163–4, samples B66, B110 and B111.

Horizon and Locality. Middle Callovian, sample B66, Wami River Area (Text-fig. 2) and Upper Tithonian, samples B110 and B111, Mandawa Anticline (Text-fig. 3).

Discussion. Grekoff (1963) records *Pirileberis prognata* from the Kimmeridgian and Portlandian of Madagascar while Guha (1975?) records it from the Callovian to Kimmeridgian of Kutch (India). Here, *P. prognata* has been found in both Middle Callovian and Upper Tithonian sediments.

Dimensions. Io.6154, male carapace (Pl. 8, fig. 10), length 0·71 mm ; height 0·43 mm ; width 0·30 mm. Io.6163, male carapace (Pl. 8, fig. 11), length 0·66 mm ; height 0·35 mm ; width 0·29 mm. Io.6164, female carapace (Pl. 8, fig. 9), length 0·66 mm ; height 0·42 mm ; width 0·29 mm.

Pirileberis ? sp.

Pl. 8, figs 3–6

Material. Five specimens, Io.6158–62, samples B110 and B111.

Horizon and Locality. Upper Tithonian, samples B110 and B111, Mandawa Anticline (Text-fig. 3).

Discussion. This new species is a rare member of the Upper Tithonian fauna which on general carapace morphology and presence of an antimerodont hinge appears to belong to *Pirileberis*. The generic assignment is queried because of the lack of information concerning the muscle scars and anterior marginal pore canals. Unlike *Pirileberis prognata* this species does not appear to be dimorphic and is also much more squat in side view.

Dimensions. Io.6158, carapace (Pl. 8, fig. 6), length 0·53 mm ; height 0·38 mm ; width 0·26 mm. Io.6159, left valve (Pl. 8, fig. 4), length 0·49 mm ; height 0·37 mm. Io.6160, carapace (Pl. 8, fig. 5), length 0·55 mm ; height 0·37 mm ; width 0·21 mm. Io.6162, carapace (Pl. 8, fig. 3), length 0·55 mm ; height 0·39 mm ; width 0·25 mm.

Family **CYTHERIDEIDAE** Sars 1925
Subfamily **CYTHERIDEINAE** Sars 1925
Genus ***AFROCYTHERIDEA*** nov.

DIAGNOSIS. Carapace thick-shelled, dimorphic, subrectangular, posteriorly tapering. Dorsal margin sinuous. Conspicuous antero-dorsal furrow below convex, projecting, anterior cardinal angle. Shell surface smooth or reticulate. Left valve larger than right. Normal pore canals large, widely spaced. Anterior marginal pore canals curved, approximately 14 in number. Hinge lobodont. Duplicature of moderate width ; no vestibule.

TYPE SPECIES. *Afrocytheridea laevigata* sp. nov.

DISCUSSION. *Afrocytheridea* gen. nov. (gender feminine) externally resembles the Bajocian/Bathonian ostracod *Eocytheridea* Bate 1964, but differs in the possession of a lobodont hinge. The anterior marginal pore canals are curved in both genera but the absence of details relating to the muscle scars of *Afrocytheridea* prevents a close phylogenetic comparison. At the present time *Afrocytheridea* is placed in the Cytherideinae rather than with *Eocytheridea* in the Schulerideidae, although it may be necessary to reassign it when details of the muscle scars become known.

Two species are assigned here to *Afrocytheridea*, *A. laevigata* sp. nov. and *A. faveolata* sp. nov., both from the Middle Callovian.

Afrocytheridea laevigata sp. nov.

Pl. 8, fig. 14 ; Pl. 9, figs 1–4 ; Text-fig. 12

DIAGNOSIS. *Afrocytheridea* without surface ornamentation.

HOLOTYPE. Io.6122, female carapace, sample B66 (Pl. 9, fig. 3).

PARATYPES. Io.6123–7, sample B66.

HORIZON AND LOCALITY. Middle Callovian, sample B66, Wami River Area (Text-fig. 2).

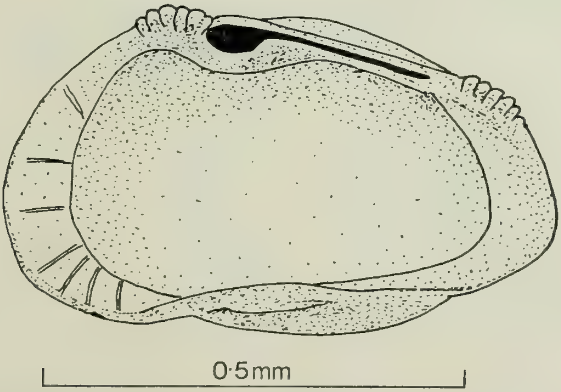

FIG. 12. *Afrocytheridea laevigata* sp. nov. Internal view, right valve, paratype Io.6126.

Description. **Carapace** outline as illustrated and showing marked sexual dimorphism. The absence of ornamentation emphasizes the deep antero-dorsal furrow and the simple normal pore canal openings. **Hinge** lobodont (Text-fig. 12), although details of the median element are obscured owing to the state of preservation. **Duplicature** of moderate width without a vestibule and with straight to slightly curved anterior **marginal pore canals** which are few in number and widely spaced. **Muscle scars** not seen.

Dimensions. Holotype. Io.6122, female carapace (Pl. 9, fig. 3), length 0·82 mm; height 0·47 mm; width 0·45 mm. Paratypes: Io.6123, female carapace (Pl. 9, fig. 1), length 0·76 mm; height 0·44 mm; width 0·44 mm. Io.6124, male carapace (Pl. 9, fig. 2), length 0·88 mm; height 0·46 mm; width 0·42 mm. Io.6125, male carapace (Pl. 8, fig. 14), length 0·88 mm; height 0·48 mm; width 0·43 mm. Io.6127, female carapace (Pl. 9, fig. 4), length 0·77 mm; height 0·43 mm; width 0·43 mm.

Discussion. This is a distinctive species superficially resembling the ostracod *Fabanella bathonica* (Oertli 1957) from the Bathonian of Europe, but it differs totally in internal details and externally in the presence of an antero-dorsal furrow.

Afrocytheridea faveolata sp. nov.

Pl. 8, figs 12, 13; Text-fig. 13a–d

Diagnosis. *Afrocytheridea* with distinct reticulate ornamentation.

Holotype. Io.6132, female right valve, sample B97 (Pl. 8, fig. 12).

Paratypes. Io.6128–31 and Io.6133, sample B97.

Horizon and Locality. Middle Callovian, samples B97 and B114. Mandawa Anticline (Text-fig. 3).

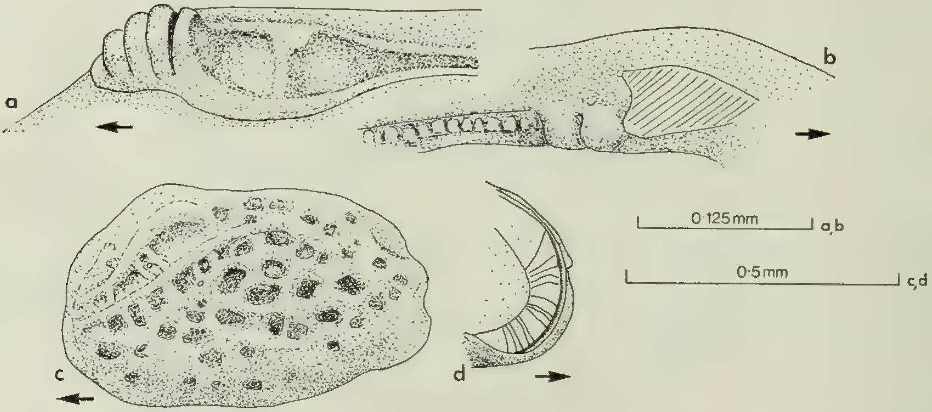

Fig. 13a–d. *Afrocytheridea faveolata* sp. nov. a. Anterior teeth and antero-median sockets, right valve hinge, paratype Io.6131. b. Anterior part of median hinge bar to show enlarged antero-median teeth, left valve, paratype Io.6133. c. External view, left valve, paratype Io.6129. d. Anterior marginal pore canals, left valve, paratype Io.6130.

DESCRIPTION. **Carapace** thick-shelled, distinctly ornamented by honeycomb-type reticulation. Spaces between reticulae upraised, forming ridges in antero-dorsal region. **Hinge** lobodont; median element denticulate with two antero-median teeth in the left valve (Text-fig. 13b), antero-median socket bifurcate (Text-fig. 13a). **Muscle scars** not seen. **Duplicature** of moderate width with some 14 curved anterior **marginal pore canals.** No vestibule.

DIMENSIONS. Holotype, Io.6132, female right valve (Pl. 8, fig. 12), length 0·73 mm; height 0·40 mm. Paratypes, Io.6128, male right valve (Pl. 8, fig. 13), length 0·77 mm; height 0·38 mm. Io.6129, female left valve (Text-fig. 13c), length 0·73 mm; height 0·44 mm.

Subfamily **GALLIAECYTHERIDEINAE** Andreev & Mandelstam 1964

Genus ***GALLIAECYTHERIDEA*** Oertli 1957

Galliaecytheridea manyuliensis sp. nov.

Pl. 9, figs 5–14; Text-fig. 14a–c

DIAGNOSIS. *Galliaecytheridea* with oval/elongate carapace tapering posteriorly with line of greatest length passing through or above mid-point. Shell surface finely pitted. Sexual dimorphism distinct. Hinge antimerodont. Curved anterior marginal pore canals, 17–19 in number.

HOLOTYPE. Io.6141, female right valve, sample B107a (Pl. 9, fig. 5).

PARATYPES. Io.6142–50, sample 107a.

HORIZON AND LOCALITY. Lower Kimmeridgian, samples B103a, B104a, B106a and B107a, Mandawa Anticline (Text-fig. 3).

DESCRIPTION. **Carapace** dimorphic, males very elongate, almost parallel-sided; females oval with sharp posterior taper. Left valve larger than right. Shell surface finely pitted. Anterior margin often with small denticles. **Hinge** antimerodont with a tendency for the antero-median teeth of the median element to increase in size (Pl. 9, figs 11–13). **Duplicature** of moderate width; the inner margin and line of concrescence coincide except antero-medially where a very narrow **vestibule** is developed (Text-fig. 14a) from which the marginal canals extend. Anterior **marginal pore canals** curved, 17–19 in number. **Muscle scars** consist of an oblique row of four round adductor scars, a large antero-dorsal frontal scar and an equally large antero-ventral mandibular scar (Pl. 9, fig. 14).

DIMENSIONS. Holotype. Io.6141, female right valve (Pl. 9, fig. 5), length 0·66 mm; height 0·37 mm. Paratypes: Io.6142, female left valve (Pl. 9, fig. 12), length 0·67 mm; height 0·43 mm. Io.6143, female right valve (Pl. 9, figs 7, 13), length 0·66 mm; height 0·37 mm. Io.6144, female left valve (Pl. 9, fig. 10), length 0·61 mm; height 0·35 mm. Io.6145, male left valve (Pl. 9, figs 11, 14), length 0·77 mm; height 0·40 mm. Io.6146, male right valve (Pl. 9, fig. 9), length 0·78 mm; height 0·37 mm. Io.6147, female left valve (Pl. 9, fig. 8), length 0·64 mm; height 0·40 mm. Io.6148, male left valve (Pl. 9, fig. 6; Text-fig. 14a), length 0·80 mm; height 0·43 mm. Io.6149, female carapace (Text-fig. 14b, c), length 0·70 mm;

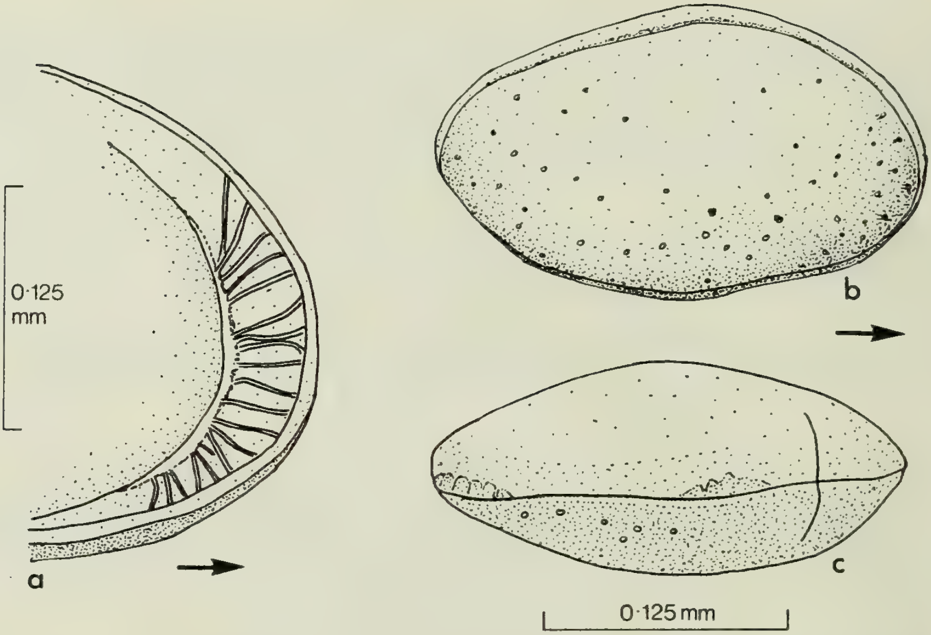

FIG. 14a–c. *Galliaecytheridea manyuliensis* sp. nov. a. Anterior duplicature and marginal pore canals, male left valve, paratype Io. 6148. b, c. Right and dorsal views, female carapace, paratype Io.6149.

height 0·43 mm ; width 0·24 mm. Io.6150, male carapace, length 0·78 mm ; height 0·42 mm ; width 0·33 mm.

DISCUSSION. *Galliaecytheridea* as diagnosed possesses a hemimerodont hinge, the median element being smooth. In *Galliaecytheridea manyuliensis* sp. nov., however, the hinge is antimerodont, the anteromedian element of which shows an increase in size of the teeth in the left valve and of the loculae in the right. Thus the hinge approaches the entomodont condition as described in *Galliaecytheridea* ? *kingscliffensis* Bate 1967, from the Bathonian of England. *G. manyuliensis* in common with *G.* ? *kingscliffensis* thus possesses a hinge differing from that described in all other species of *Galliaecytheridea*, although both species have the other morphological characters of the genus. The introduction of a subgeneric unit at this stage does not, however, appear to be necessary.

The lateral outline of the female dimorph is generally most useful in distinguishing between species of *Galliaecytheridea* and in this respect *G. manyuliensis* is easily separated from the more squat and robust *G.* ? *kingscliffensis*. *G. remota* Grekoff 1963, from the Callovian of Madagascar, differs in having a more pointed posterior end as well as a different hinge.

G. manyuliensis sp. nov. derives its name from the Manyuli stream, Mandawa Anticline.

Family **PROTOCYTHERIDAE** Ljubimova 1955

Genus ***PROCYTHERIDEA*** Peterson 1954

The incorrect assignment of a large number of species in the European Mesozoic to this genus has been dealt with fully by Bate (1963 : 214) and Lord (1972 : 326). The genus is thus restricted to species having a triangular lateral outline. *Procytheridea* was placed in the family Protocytheridae in Moore (1961 : 330) and this assignment is retained here.

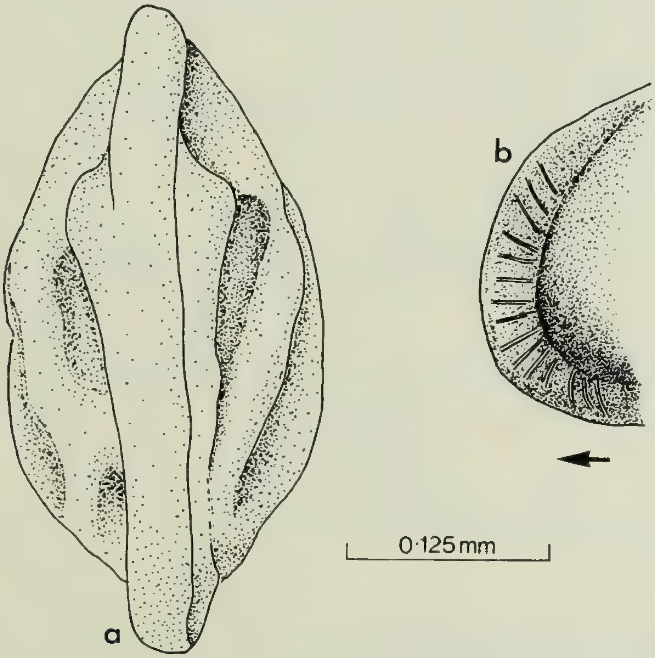

FIG. 15a, b. *Procytheridea disparlateralis* sp. nov. Dorsal and anterior end to show marginal pore canals, carapace, paratype Io.6136.

Procytheridea disparlateralis sp. nov.

Pl. 8, figs 7, 8 ; Text-fig. 15a, b

DIAGNOSIS. *Procytheridea* with single oblique ridge bounded by two depressions on right valve, and with tri-radiate ridge pattern on left valve.

HOLOTYPE. Io.6135, sample B97 (Pl. 8, fig. 7).

PARATYPES. Io. 6134 and Io.6136, sample B97.

HORIZON AND LOCALITY. Middle Callovian, sample B97, Mandawa Anticline (Text-fig. 3).

Description. **Carapace** triangular with larger left valve possessing a triradiate ridge pattern and the smaller right valve having a single oblique ridge with a broad shallow depression on either side. The absence of a ventro-lateral depression in the right valve produces this variation of ornamentation. **Eye swelling** situated in the region of the anterior cardinal angle, particularly visible in dorsal view (Text-fig. 15a). Internal details not known apart from the anterior **marginal pore canals** as seen from the exterior (Text-fig. 15b).

Dimensions. Holotype, Io.6135, carapace (Pl. 8, fig. 7), length 0·46 mm ; height 0·27 mm ; width 0·24 mm. Paratype, Io.6134, carapace (Pl. 8, fig. 8), length 0·44 mm ; height 0·25 mm ; width 0·20 mm.

Discussion. *Procytheridea disparlateralis* sp. nov. is so named because of the difference in ornamentation between the right and the left valve. It is similar in both ornamentation and shell outline to *Progonocythere falcula* Grekoff 1963, from the Callovian of Madagascar ; it also resembles Ostracod Nr. 4 of Lutze (Simon & Bartenstein 1962), from the Callovian of Germany, and less closely *Procytheridea martini* Bizon 1958, from the Oxfordian of France and Switzerland (Oertli 1959). Although morphologically close to these species *Procytheridea disparlateralis* may be distinguished from all three by its ridge pattern and associated shell depressions.

Family **TRACHYLEBERIDIDAE** Sylvester-Bradley 1948

Genus ***CYTHERETTA*** Müller 1894

'*Cytheretta*' sp.

Pl. 10, figs 1, 2

Material. A single carapace, Io.6173, sample B114.

Horizon and Locality. Middle Callovian, sample B114, Mandawa Anticline (Text-fig. 3).

Discussion. No internal details of this ostracod are available. Externally it closely resembles species of *Cytheretta* Müller 1894 and *Paracytheretta* Triebel 1941. The present species is considerably older than the known ranges of these two genera and could be an ancestral form.

Progonocythere grumosa Ljubimova & Mohan 1960, from the Callovian of India (Kutch), has some similarity of outline but lacks the postero-dorsal projection of '*Cytheretta*' and most probably belongs to the genus *Protocythere*, although no internal details were recorded.

Dimensions. Io.6173, carapace, length 0·54 mm ; height 0·31 mm ; width 0·28 mm.

Genus ***MANDAWACYTHERE*** nov.

Type Species. *Mandawacythere striata* sp. nov.

Diagnosis. Trachyleberididae having elongate dimorphic carapace. Left valve larger than right. Hinge lophodont. Duplicature anteriorly possessing small vestibule and few, straight marginal pore canals. Muscle scars having ventro-median adductor scar divided ; large frontal scar with smaller scar situated in front and small antero-ventral mandibular scar.

DISCUSSION. *Mandawacythere* gen. nov. (gender feminine), named after its location in the Mandawa region, is placed here in the Trachyleberididae on the muscle scar pattern. This assignment should, however, be considered as tentative at the present time. Certainly it is not possible to place *Mandawacythere* in any of the subfamily groups listed by Hazel (1967) for either the trachyleberids or the hemicytherids. The absence of a subcentral tubercle together with the divided adductor scar could lend weight to the consideration of *Mandawacythere* as being an early hemicytherid, but the simple lophodont hinge and limited number of marginal pore canals make any definite assignment difficult.

Mandawacythere striata sp. nov.

Pl. 10, figs 3–10 ; Text-fig. 16a–b

1963 Ostracod 38a Grekoff : 1759, pl. 10, figs 248-9.

DIAGNOSIS. *Mandawacythere* having 10–11 low, longitudinal ridges confluent at their posterior ends. Shell surface punctuate.

HOLOTYPE. Io.6174, right valve, sample B219 (Pl. 10, figs 3, 4, 10 ; Text-fig. 16b).

PARATYPES. Io.6175–81, samples B219 and B223.

HORIZON AND LOCALITY. (?) Lower Tithonian, samples B219 and B223, Mandawa Anticline (Text-fig. 3).

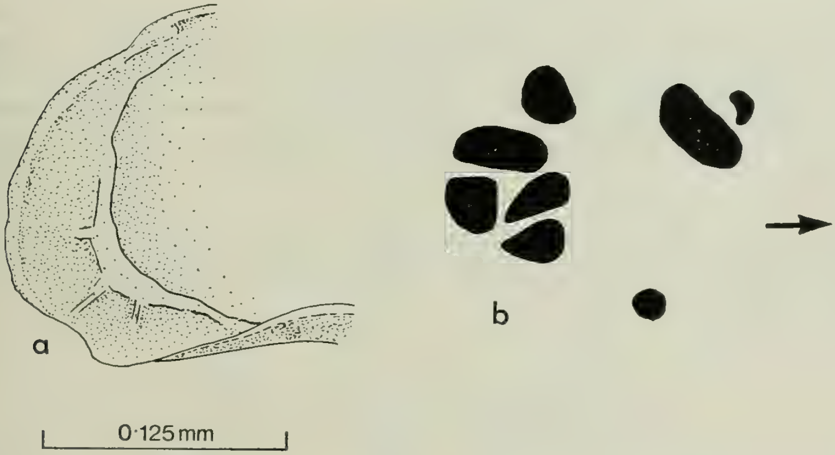

FIG. 16a, b. *Mandawacythere striata* sp. nov. a. Anterior duplicature, female right valve, paratype Io.6181. b. Muscle scars, female right valve, holotype Io.6174. × 735.

Description. **Carapace** elongate, especially in the male. Male dimorph having 10 longitudinal lateral ridges, female dimorph 11. Interspaces between ridges punctate. **Hinge** lophodont with very long median element. **Duplicature** not clearly seen although in one specimen a small anterior vestibule is present together with a few, straight, **marginal pore canals** (Text-fig. 16a). **Muscle scars** consist of four adductor scars of which the ventro-median scar is divided ; the frontal scar is large, oval, with a small ancillary scar in front ; mandibular scar small, situated antero-ventrally (Pl. 10, fig. 10 ; Text-fig. 16b).

Dimensions. Holotype, Io.6174, female right valve (Pl. 10, figs 3, 4, 10 ; Text-fig. 16b), length 0·37 mm ; height 0·19 mm. Paratypes : Io.6175, male right valve (Pl. 10, figs 8, 9), length 0·43 mm ; height 0·19 mm. Io.6176, juvenile ? right valve (Pl. 10, fig. 7), length 0·29 mm ; height 0·15 mm. Io.6177, female carapace (Pl. 10, fig. 5), length 0·35 mm ; height 0·17 mm ; width 0·15 mm. Io.6178, female carapace (Pl. 10, fig. 6), length 0·34 mm ; height 0·17 mm ; width 0·17 mm.

Discussion. *Mandawacythere striata* sp. nov. is totally unlike any previously described species with the exception of Ostracod 38a of Grekoff (1963), recorded from the Kimmeridgian of Madagascar and by Guha (1975?) from the Kimmeridgian to Portlandian of Kutch (India). Ostracod 38a, however, has fewer lateral ridges and appears to be closer to the paratype Io.6176 (Pl. 10, fig. 7), considered here to be a possible juvenile instar. Should this prove not to be so it will be necessary to remove this specimen from the species, and Ostracod 38a from the synonymy.

Family **UNCERTAIN**

Genus ***RHADINOCYTHERE*** nov.

Derivation of Name. Greek, ῥαδινός, slender, +*cythere*. Gender, feminine.

Type Species. *Rhadinocythere gracilis* sp. nov.

Diagnosis. Small (length c 0·41 mm) genus of Cytheracea having very slender carapace (width c 0·12 mm) highest at anterior half. Lateral surface punctate and with three primary lateral ridges. Anterior duplicature with median vestibule ; marginal pore canals straight, few in number. Hinge lophodont. Left valve larger than right.

Discussion. This distinct and small ostracod is recorded only from the Middle or Upper Kimmeridgian of the Mandawa Anticline Area. Unfortunately no details of the muscle scars have been seen thus making it impossible to assign the genus to a known family.

Rhadinocythere gracilis sp. nov.

Pl. 10, figs 11–14 ; Pl. 11, figs 1–4 ; Text-fig. 17

Diagnosis. *Rhadinocythere* with three primary lateral ridges and two subordinate ridges interleaved in anterior half.

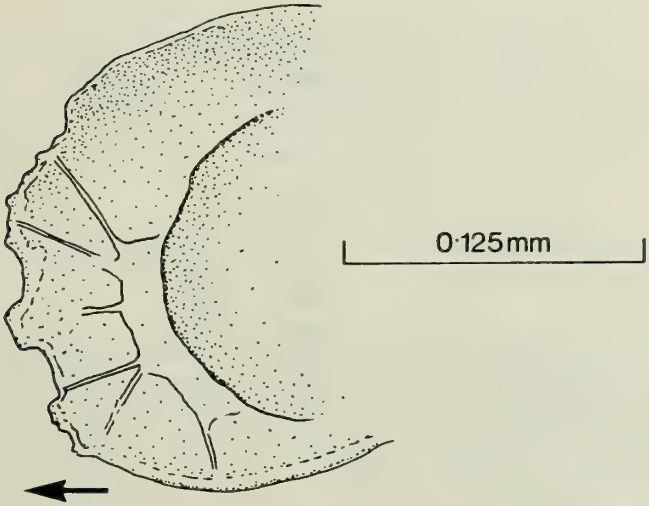

FIG. 17. *Rhadinocythere gracilis* sp. nov. Anterior duplicature with vestibule and marginal pore canals, right valve, paratype Io.6188.

HOLOTYPE. Io.6182, carapace, sample B223 (Pl. 10, fig. 14).

PARATYPES. Io.6183–9, sample B223.

HORIZON AND LOCALITY. Middle or Upper Kimmeridgian, samples B219 and B223, Mandawa Anticline (Text-fig. 3).

DESCRIPTION. **Carapace** oval, highest at anterior end; slender in dorsal or ventral view. Shell surface finely punctate; additional ornamentation consisting of three primary lateral ridges extending for the greater part of the length of the valve and having two subordinate ridges interleaved in the anterior half. **Hinge** lophodont with long median element. **Muscle scars** not seen. Anterior **duplicature** broad with distinct vestibule (Text-fig. 17). **Marginal pore canals** few in number and straight (Text-fig. 17).

DIMENSIONS. Holotype, Io.6182, carapace (Pl. 10, fig. 14), length 0·41 mm; height 0·21 mm; width 0·14 mm. Paratypes: Io.6183, carapace (Pl. 11, fig. 4), length 0·37 mm; height 0·17 mm; width 0·12 mm. Io.6184, carapace (Pl. 10, fig. 11), length 0·38 mm; height 0·18 mm; width 0·11 mm. Io.6185, right valve (Pl. 10, fig. 13; Pl. 11, figs 1, 2), length 0·38 mm; height 0·18 mm. Io.6186, left valve (Pl. 10, fig. 12), length 0·38 mm; height 0·19 mm. Io.6187, carapace (Pl. 11, fig. 3), length 0·34 mm; height 0·17 mm; width 0·12 mm.

DISCUSSION. No ostracod comparable at either generic or specific level is known from the Mesozoic around the Indian Ocean. From its size and rather delicate shell structure *Rhadinocythere gracilis* sp. nov. was most probably a phytal dweller.

Family **CYTHERURIDAE** Müller 1894

Subfamily **CYTHERURINAE** Müller 1894

Genus ***EUCYTHERURA*** Müller 1894

Eucytherura sp.

Pl. 11, figs 5, 6

Material. A single left valve, Io.6190, sample B97.

Horizon and Locality. Middle Callovian, sample B97, Mandawa Anticline (Text-fig. 3).

Discussion. A single left valve, highly ornamented and having a low eye swelling below the anterior cardinal angle. Internally the hinge is rather poorly preserved but the median bar appears to be denticulate. The duplicature lacks a vestibule.

The earliest recorded appearance of *Eucytherura* still remains from the Upper Lias of England (Bate & Coleman 1975).

Dimensions. Io.6190, left valve, length 0·39 mm ; height 0·23 mm.

Genus ***PROCYTHERURA*** Whatley 1970 emend. Bate & Coleman 1975

In the original diagnosis the hinge was recorded as lophodont and the frontal muscle scar as heart-shaped. The hinge in *Procytherura* is in fact entirely smooth but has the ends of the median element expanded, thereby becoming holoperatodont (Bate 1972 : 45) rather than lophodont. The frontal muscle scar varies from heart-shaped to V-shaped. The genus has a known range of Lower Jurassic (Bate & Coleman 1975) to Upper Jurassic (Whatley 1970) in Great Britain and here is recorded from the Upper Jurassic of Tanzania.

Procytherura aerodynamica sp. nov.

Pl. 11, figs 7–16 ; Pl. 12, figs 1–3 ; Text-fig. 18a–c

1974 Indet. sp. E. Oertli : 949, pl. 7, fig. 5.

Diagnosis. *Procytherura* having stream-lined carapace outline, slightly alate postero-ventrally. Shell surface decorated with large pits and fine puncta.

Holotype. Io.6191, male carapace, sample B219 (Pl. 11, fig. 7).

Paratypes. Io.6192–208, samples B219 and B223.

Horizon and Locality. Lower and Middle or Upper Kimmeridgian, samples B103a, B219, B222 and B223, Mandawa Anticline (Text-fig. 3).

Description. **Carapace** oval in adult dimorphs with a gradual taper towards the posterior end. In juvenile instars the dorsal margin is more strongly curved producing a distinct caudal process (Pl. 11, figs 10, 11). The posterior ventro-lateral alation of the carapace is more strongly developed in the adult instar. Left valve larger than the right. Cardinal angles distinct ; no eye swelling. Shell surface ornamented with a fine punctation and, in adult instars, larger pits (Pl. 11, figs 7, 8,

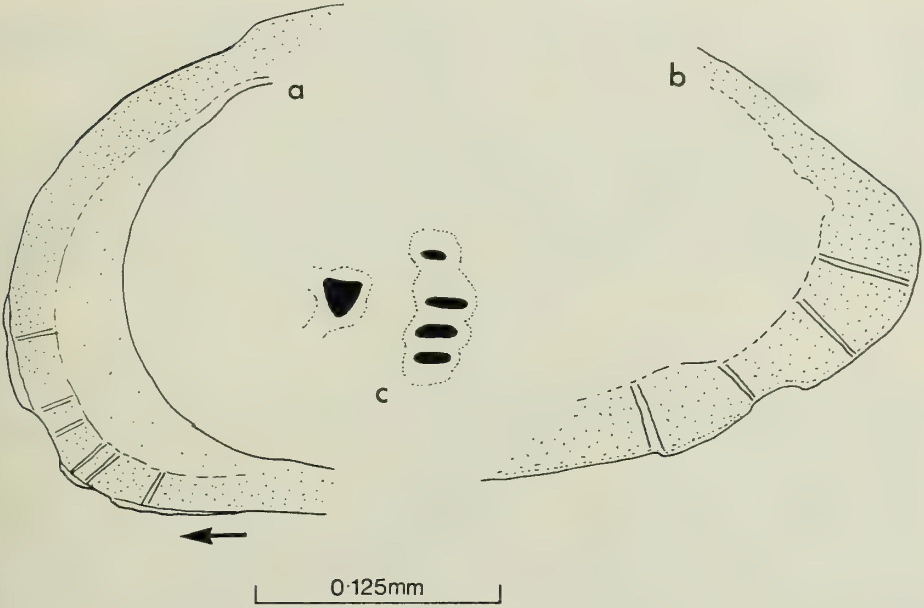

Fig. 18a–c. *Procytherura aerodynamica* sp. nov. a, b. Anterior duplicature with vestibule and marginal pore canals and posterior duplicature, male right valve, paratype Io.6208. c. Muscle scars, female right valve, paratype Io.6207.

12, 13). The juveniles possess the fine puncta only. **Hinge** holoperatodont; median element long, smooth and expanded at both ends. **Duplicature** broad with large anterior vestibule. No posterior vestibule present. **Marginal pore canals** straight, few in number. Anterior with narrow **flange** (Text-fig. 18a). **Muscle scars** consist of four oval, rather elongate adductor scars with a large heart-shaped frontal scar.

Dimensions. Holotype, Io.6191, male carapace (Pl. 11, fig. 7), length 0·54 mm; height 0·27 mm; width 0·21 mm. Paratypes: Io.6192, female carapace (Pl. 11, fig. 8), length 0·50 mm; height 0·26 mm; width 0·22 mm. Io.6193, female right valve (Pl. 11, fig. 13), length 0·50 mm; height 0·26 mm. Io.6194, male carapace (Pl. 12, fig. 2), length 0·56 mm; height 0·27 mm; width 0·21 mm. Io.6195, juvenile carapace (Pl. 12, fig. 3), length 0·46 mm; height 0·24 mm; width 0·18 mm. Io.6196, female right valve (Pl. 11, fig. 15), length 0·49 mm; height 0·26 mm. Io.6197, male left valve (Pl. 11, fig. 14), length 0·54 mm; height 0·27 mm. Io.6198, female left valve (Pl. 12, fig. 1), length 0·46 mm; height 0·24 mm. Io.6199, juvenile right valve (Pl. 11, fig. 9), length 0·42 mm; height 0·24 mm. Io.6200, juvenile right valve (Pl. 11, figs 10, 16), length 0·44 mm; height 0·23 mm. Io.6202, male right valve (Pl. 11, fig. 12), length 0·51 mm; height 0·24 mm. Io.6203, juvenile left valve (Pl. 11, fig. 11), length 0·47 mm; height 0·22 mm.

Discussion. *Procytherura aerodynamica* sp. nov. differs from European species of the genus by lacking the lateral ridges or reticulation found in all species so far described. The eye swelling and dorso-median sulcation are also missing but despite this it is preferred to place *aerodynamica* in *Procytherura* until the description of further species shows whether the genus should be more broadly diagnosed or subdivided.

Indet. sp. E described by Oertli (1974) from core 30, site 260 off Western Australia is conspecific with *P. aerodynamica.* This has been confirmed by Oertli (personal communication) from material subsequently sent to him. The geographical range of *P. aerodynamica* is thus extended. The sample from which Indet. sp. E was recovered may now, almost certainly, be regarded as being of Kimmeridgian age.

Procytherura sp.

Pl. 12, fig. 4

Material. A single carapace, Io.6209, sample B97.

Horizon and Locality. Middle Callovian, sample B97, Mandawa Anticline (Text-fig. 3).

Discussion. That this rare ostracod is more closely allied to the European species of *Procytherura* than it is to the Tanzanian *P. aerodynamica* is evidenced by the surface ornamentation of low, evenly spaced lateral ridges and, in dorsal view, a distinct median constriction. An eye swelling might be present here but the preservation of the specimen makes this difficult to determine. No internal details have been observed.

Dimensions. Io.6209, carapace, length 0·30 mm; height 0·15 mm; width 0·12 mm.

Subfamily **CYTHEROPTERINAE** Hanai 1957

Genus ***CYTHEROPTERON*** Sars 1866

Subgenus ***INFRACYTHEROPTERON*** Kaye 1964

Cytheropteron (? Infracytheropteron) aitkeni sp. nov.

Pl. 12, figs 5–13; Text-fig. 19a–c

Diagnosis. Dimorphic species of *Cytheropteron* having simple hinge consisting of smooth groove in left valve articulating with dorsal bar in right valve. Carapace strongly alate with broad median sulcus. Eye swelling indistinct, lacking or strongly developed. Shell surface pitted. Left valve overlapping right along dorsal margin. Inner margin and line of concrescence coincide.

Holotype. Io.6210, female left valve, sample B219 (Pl. 12, fig. 7).

Paratypes. Io.6211–19 and Io.6240, samples B219, B223, B104a, and 107a.

Horizon and Locality. Lower and Middle or Upper Kimmeridgian, samples B219, B223, B107a and B104a, Mandawa Anticline (Text-fig. 3).

Description. **Carapace** subrectangular with broad alae and wide median sulcus. Ala terminating in a spine. Anterior and posterior margins sometimes denticulate (Pl. 12, figs 8, 12). Male dimorph more elongate than female. Left valve overlaps

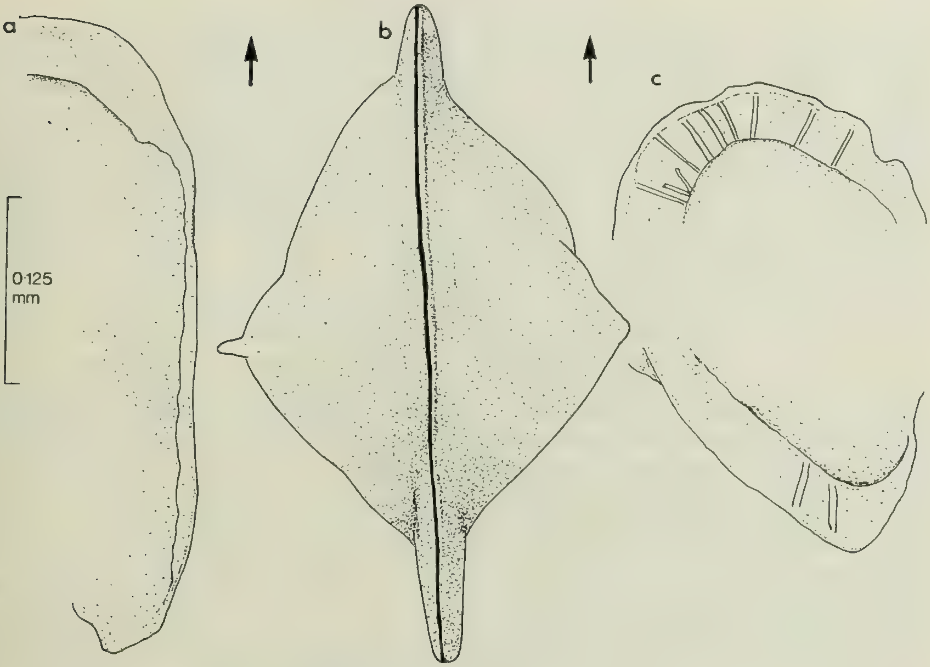

FIG. 19a–c. *Cytheropteron* (? *Infracytheropteron*) *aitkeni* sp. nov. a. Internal view, male right valve dorsal margin and duplicature, paratype Io.6216. b. Dorsal view, female carapace, paratype Io.6211. c. Anterior and posterior duplicatures to show marginal pore canals, female right valve, paratype Io.6240.

right dorsally (Pl. 12, fig. 8) but ventrally there is no overlap (Text-fig. 19b). Shell surface pitted with furrow parallel to dorsal margin. **Eye swelling** usually poorly developed but may be prominent (Pl. 12, fig. 9). **Hinge** consisting of a long, smooth groove in the left valve into which fits the dorsal bar of the right valve, slightly downset from the dorsal edge of the valve (Pl. 12, fig. 12). **Duplicature** of moderate width with inner margin and line of concrescence coinciding. Approximately 9 straight anterior **marginal pore canals** and about 2 posterior canals (Text-fig. 19c). **Muscle scars** consist of an oblique row of four oval to rounded adductor scars with a large V-shaped frontal scar (Pl. 12, fig. 13).

DIMENSIONS. Holotype, Io.6210, female left valve (Pl. 12, fig. 7), length 0·39 mm ; height 0·24 mm. Paratypes : Io.6211, female carapace (Pl. 12, fig. 8 ; Text-fig. 19b), length 0·43 mm ; height 0·26 mm ; width 0·27 mm ; Io.6212, male left valve (Pl. 12, fig. 11), length 0·43 mm ; height 0·22 mm. Io.6213, female right valve (Pl. 12, fig. 6), length 0·37 mm ; height 0·21 mm. Io.6214, female left valve (Pl. 12, figs 10, 13), length 0·42 mm ; height 0·24 mm. Io.6215, female left valve (Pl. 12, fig. 9), length 0·37 mm ; height 0·21 mm. Io.6216, male right valve (Pl. 12, fig. 12), length 0·38 mm ; height 0·17 mm. Io.6217, juvenile left valve (Pl. 12, fig. 5), length 0·31 mm ; height 0·18 mm.

Discussion. *Cytheropteron* (? *Infracytheropteron*) *aitkeni* sp. nov. is named after Dr W. G. Aitken, formerly geologist with the Tanganyika Geological Survey.

This species is placed in the subgenus *Infracytheropteron* with a query for two reasons. Firstly, an eye swelling, a feature not so far recorded in species of this subgenus, is present ; secondly, the hinge, although having smooth elements, is of the adont and not of the holoperatodont type. The external appearance of *C.* (? *I.*) *aitkeni* sp. nov. is such that it closely resembles the European Lower Jurassic *Cytheropteron* (*Cytheropteron*) *alafastigatum* Fischer 1962 but is distinguished by its hinge and the development of an eye swelling.

Cytheropteron (Infracytheropteron) ndaui sp. nov.

Pl. 13, figs 5–10 ; Text-fig. 20a–e

Diagnosis. Small dimorphic species of *Infracytheropteron* having rectangular outline and broadly arched dorsal margin ; keel-like alae producing broad, flattened venter in female, venter convex in male.

Holotype. Io.6225, female carapace, sample B223 (Pl. 13, fig. 5).

Paratypes. Io.6226–9 and Io.6232, sample B223.

Horizon and Locality. Middle or Upper Kimmeridgian, samples B219 and B223, Mandawa Anticline (Text-fig. 3).

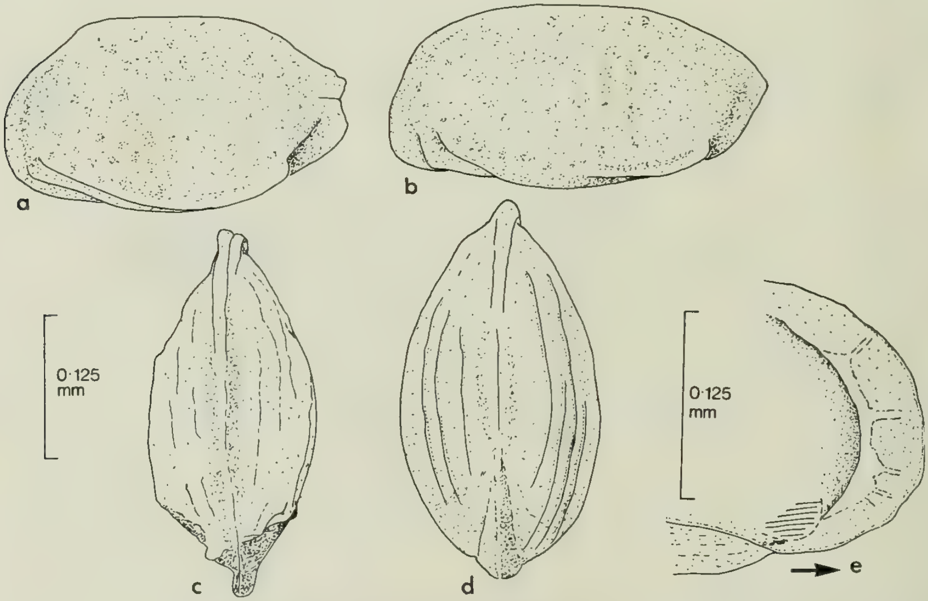

Fig. 20a–e. *Cytheropteron* (*Infracytheropteron*) *ndaui* sp. nov. a. External view, female left valve, paratype Io.6226. b. External view, male left valve, paratype Io.6229. c. Ventral view, female carapace, holotype Io.6225. d. Ventral view, male carapace, paratype Io.6227. e. Anterior duplicature, vestibule and pore canals, female left valve, paratype Io.6232.

DESCRIPTION. **Carapace** rectangular in outline; males more elongate than females. Both dimorphs convex in dorsal view; males convex in ventral view, females with flattened venter (Text-fig. 20c, d). Alae keel-like, bordering venter. Caudal process more pronounced in female dimorph. Dorsal margin very broadly arched with distinct cardinal angles. Left valve larger than the right. **Hinge** holoperatodont: terminal teeth of right valve smooth; median groove terminally expanded, smooth. Left valve with complementary smooth structures although the median bar is rather worn in the material available. **Duplicature** of moderate width: the inner margin and line of concrescence do not coincide anteriorly and a narrow vestibule is present (Text-fig. 20e). **Marginal** pore canals short, straight and few in number. **Muscle scars** not seen.

DIMENSIONS. Holotype. Io.6225, female carapace (Pl. 13, fig. 5; Text-fig. 20c), length 0·35 mm; height 0·20 mm; width 0·17 mm. Paratypes: Io.6226, female left valve (Pl. 13, figs 6, 8; Text-fig. 20a), length 0·34 mm; height 0·19 mm. Io.6227, male carapace (Pl. 13, fig. 10; Text-fig. 20d), length 0·38 mm; height 0·20 mm; width 0·20 mm. Io.6228, female right valve (Pl. 13, fig. 7), length 0·32 mm; height 0·17 mm. Io.6229, male left valve (Pl. 13, fig. 9; Text-fig. 20b), length 0·37 mm; height 0·18 mm.

DISCUSSION. *Cytheropteron* (*Infracytheropteron*) *ndaui* sp. nov. is named after Mr Alfred Ndau, Field Assistant with the Tanganyika Geological Survey during the 1965 BMNH expedition to Tanzania. The species differs from others of the subgenus on the combination of shape, keel-like alae and ornamentation.

Subgenus **Uncertain**

Cytheropteron grekoffi sp. nov.

Pl. 12, fig. 14; Pl. 13, figs 1, 2

DIAGNOSIS. Oval species of *Cytheropteron* having narrowly rounded posterior end lacking a caudal process. Shell surface coarsely pitted. Marginal borders broad.

HOLOTYPE. Io.6220, carapace, sample BM86 (Pl. 13, fig. 1).

PARATYPES. Io.6221–4, samples B2 and B67.

HORIZON AND LOCALITY. Upper Oxfordian, samples BM86, B2 and B67, Wami River Area (Text-fig. 2).

DESCRIPTION. **Carapace** lacking caudal process, oval in outline. Ventrolateral border convex rather than alate, overhanging ventral surface. Shell ornamented with large pits. Broad marginal border extends around anterior, along venter and around posterior end. **Internal details** not known.

DIMENSIONS. Holotype. Io.6220, carapace (Pl. 13, fig. 1), length 0·50 mm; height 0·30 mm; width 0·25 mm. Paratypes: Io.6221, carapace (Pl. 13, fig. 2), length 0·41 mm; height 0·26 mm; width 0·18 mm. Io.6222, carapace (Pl. 12, fig. 14), length 0·41 mm; height 0·26 mm; width 0·23 mm.

DISCUSSION. *Cytheropteron grekoffi* sp. nov. cannot yet be placed in any of the subgenera of *Cytheropteron* owing to the absence of internal information. Externally this species is closely similar to *Cytheropteron* 1040 of Grekoff (1963), from the Kimmeridgian of Madagascar, but tends to be more robust, differing in having a more obliquely angled postero-ventral border.

Cytheropteron sp.

Pl. 13, figs 3, 4

MATERIAL. Two specimens, Io.6230–1, sample B223.

HORIZON AND LOCALITY. Middle or Upper Kimmeridgian, sample B223, Mandawa Anticline (Text-fig. 3).

DISCUSSION. *Cytheropteron* sp. bears some similarity to *Cytheropteron corrosum* Grekoff 1963, from the Portlandian of Madagascar, but is more elongate in outline and has a different ornamental pattern of pits.

DIMENSIONS. Io.6230, carapace (Pl. 13, fig. 4), length 0·32 mm ; height 0·16 mm ; width 0·13 mm. Io.6231, carapace (Pl. 13, fig. 3), length 0·32 mm ; height 0·17 mm ; width 0·13 mm.

Genus ***PARACYTHERIDEA*** Müller 1894

Paracytheridea mandawaensis sp. nov.

Pl. 14, figs 1–9

DIAGNOSIS. *Paracytheridea* having elongate carapace with short, rather broad alae. Shell ornamented with three carinae : dorsal, oblique median and ventro-lateral. Shell surface reticulate ; reticulae having secondary reticulation.

HOLOTYPE. Io.6233, carapace, sample B223 (Pl. 14, figs 1, 6).

PARATYPES. Io.6234–9, sample B223.

HORIZON AND LOCALITY. Middle or Upper Kimmeridgian, samples B219 and B223, Mandawa Anticline Area (Text-fig. 3).

DESCRIPTION. **Carapace** outline as illustrated. The alae are rather short and broad with their greatest development in the posteroventro-lateral region. This produces a flat ventral surface widening towards the posterior end. Carapace convex in dorsal view. **Ornamentation** consists of a basic surface reticulation, the reticulae of which possess secondary reticulae (Pl. 14, fig. 5). Three longitudinal carinae, the lowermost extending along the ala to meet the anterior margin in the ventral half of the valve. The median carina extends obliquely across the valve and in some specimens (Pl. 14, figs 1, 3) is complete, while in others (Pl. 14, figs 2, 4) it is discontinuous, forming a plexus of carinae. The dorsal-most carina extends along the dorsal margin, cuts through the eye node and joins the anterior margin in the dorsal half of the valve ; posteriorly the dorsal carina fuses with the median carina at the posterior cardinal angle in most valves (Pl. 14, figs 1, 2, 4) but not in specimen Io.6235 (Pl. 14, fig. 3). **Eye node** distinct, set back from the anterior cardinal angle in the holotype (Pl. 14, fig. 1) but may be situated much closer to it in some individuals (Pl. 14, fig. 3). **Hinge** difficult to determine because of the state of preservation : in the left valve the terminal elements appear to be loculate but the median bar is too eroded to identify with certainty ; hinge details not observed in the right valve. **Muscle scars** consist of an oblique row of four elongate adductor scars with a large V-shaped frontal scar (Pl. 14, fig. 6). **Duplicature** of moderate width with the inner margin and line of concrescence coinciding. **Marginal pore canals** have not been observed.

DIMENSIONS. Holotype, Io.6233, carapace (Pl. 14, figs 1, 6), length 0·36 mm ; height 0·17 mm ; width 0·15 mm. Paratypes : Io.6234, right valve (Pl. 14, fig. 2), length 0·37 mm ; height 0·18 mm. Io.6235, left valve (Pl. 14, figs 3, 6), length 0·35 mm ; height 0·17 mm. Io.6236, carapace (Pl. 14, fig. 7), length 0·35 mm ; height 0·16 mm ; width 0·15 mm. Io.6237, carapace (Pl. 14, fig. 8), length 0·35 mm ; height 0·17 mm ; width 0·17 mm. Io.6238, left valve (Pl. 14, fig. 9), length 0·36 mm ; height 0·16 mm. Io.6239, carapace (Pl. 14, fig. 4), length 0·38 mm ; height 0·19 mm ; width 0·17 mm.

DISCUSSION. *Paracytheridea mandawaensis* sp. nov. is very close to *Orthonotacythere* (*Acrocythere*) 129 described by Grekoff (1963), from the Portlandian of Madagascar, in both size and general appearance. There are, however, some differences, namely the absence of an eye node and a dorsal carina in Grekoff's species which indicate that the two are not conspecific.

Subfamily **UNCERTAIN**

Genus ***ACROCYTHERE*** Neale 1960

Acrocythere ? tricostata sp. nov.

Pl. 13, figs 11–14 ; Text-fig. 21

DIAGNOSIS. Species placed with query in *Acrocythere*, having three longitudinal carinae of which the median carina has a double U-bend at valve centre. Shell surface smooth.

HOLOTYPE. Io.6241, left valve, sample B223 (Pl. 13, fig. 11).

PARATYPES. Io.6242–5, samples B219 and B223.

HORIZON AND LOCALITY. Middle or Upper Kimmeridgian, samples B219 and B223, Mandawa Anticline (Text-fig. 3).

DESCRIPTION. **Carapace** small, oval in outline with distinct posterior taper. In the right valve a concave postero-dorsal slope produces a short narrowly rounded caudal process. The outline of the left valve, as illustrated (Pl. 13, fig. 11), is considerably different and the line of greatest length is situated higher up on the valve than in the right. **Ornamentation** consists of three longitudinal carinae that converge towards the anterior margin. The dorsal carina follows the dorsal and the antero-dorsal margins, passing through the eye node. The median carina is obliquely orientated and sinuous ; the sinuosity producing two U-shaped bends at about valve centre. The lowermost carina follows the outer edge of the wing-like

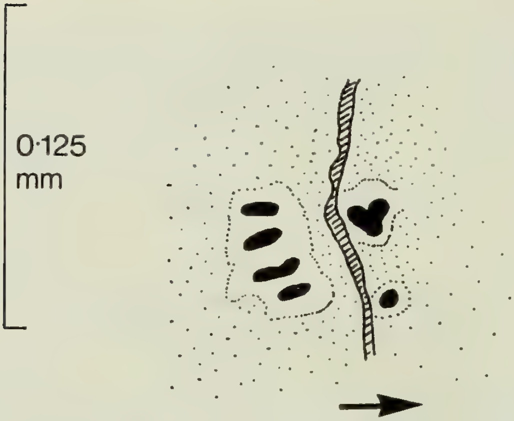

FIG. 21. *Acrocythere* ? *tricostata* sp. nov. Muscle scars, external view, right valve, paratype Io.6245.

development of the valve. **Hinge** appears to be holoperatodont, curved and almost sinuous. All elements are smooth, with the median element expanded terminally (Pl. 13, fig. 12). The apparent absence of dentition may be because of the state of preservation but at the same time no loculae have been observed. **Duplicature** rather broad ; inner margin and line of concrescence coinciding. **Marginal pore canals** long and straight, few in number although the precise number has not been observed. **Muscle scars** consist of a slightly curved row of four oval adductor scars with an antero-dorsal V-shaped frontal scar and a small, round, antero-ventral mandibular scar.

DIMENSIONS. Holotype, Io.6241, left valve (Pl. 13, fig. 11), length 0·35 mm ; height 0·20 mm. Paratypes : Io.6242, left valve (Pl. 13, fig. 13), length 0·35 mm ; height 0·19 mm. Io.6243, right valve (Pl. 13, fig. 14), length 0·37 mm ; height 0·21 mm. Io.6244, right valve (Pl. 13, fig. 12), length 0·37 mm ; height 0·21 mm.

DISCUSSION. The carapace outline, rather sigmoid dorsal margin and median hinge element, together with the presence of three lateral ridges and absence of reticulation, sets *Acrocythere* ? *tricostata* sp. nov. apart from all other species of the genus. Although species of *Acrocythere* in general possess only two lateral ridges, close examination of the type species reveals a tendency to develop a dorsal structure. Because of this it is preferred to place the present species in *Acrocythere* with a query rather than to erect a new genus at this time. The probability that a new genus may be necessary for this southern hemisphere species is, however, accepted.

Genus ***LOONEYELLA*** Peck 1951

Looneyella africana sp. nov.

Pl. 14, figs 10–12 ; Text-fig. 22a–d

DIAGNOSIS. *Looneyella* having five tubercles : two situated in postero-dorsal region, one antero-median and one antero-dorsal in position. A fifth tubercle is situated at postero-ventral termination of broad, curved ridge extending down from eye node. Shell surface reticulate.

HOLOTYPE. Io.6246, left valve, sample B223 (Pl. 14, fig. 10).

PARATYPES. Io.6247–50, samples B219 and B223.

HORIZON AND LOCALITY. Middle or Upper Kimmeridgian, samples B219 and B223, Mandawa Anticline (Text-fig. 3).

DESCRIPTION. **Carapace** dimorphic, quadrate to rectangular in outline ; broadly rounded anteriorly, posterior end triangular. Line of greatest length situated in dorsal third of carapace. **Ornamentation** consisting of four distinct tubercles as diagnosed (Text-fig. 22a, b). Shell surface coarsely reticulate, the reticulae passing over the tubercles (Pl. 14, fig. 10). **Hinge** poorly preserved ; left valve with terminal locellate sockets and a median bar, right valve with complementary structures. The median bar of the left valve appears to be smooth but this may be due to the state of preservation. **Duplicature** broad : inner margin and line of concrescence coincide. **Marginal pore canals** long and straight : 6 anteriorly and 3 posteriorly (Text-fig. 22c, d). **Muscle scars** not seen.

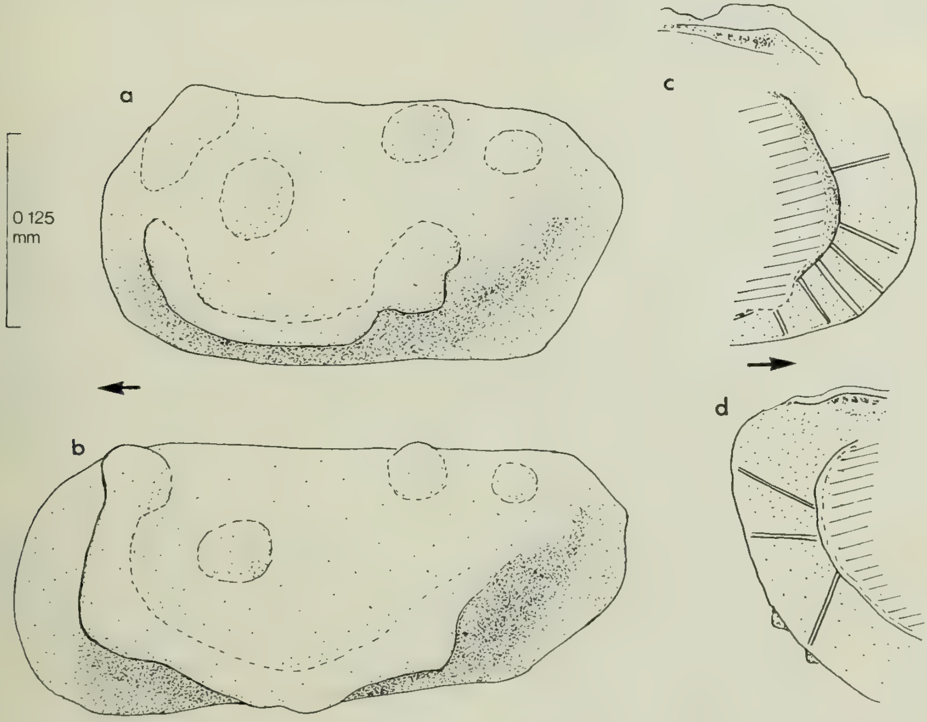

FIG. 22a–d. *Looneyella africana* sp. nov. a. External view, female left valve, holotype Io.6246. b. External view, male left valve, paratype Io.6248. c, d. Anterior and posterior duplicatures with marginal pore canals, female left valve, paratype Io.6249.

Dimensions. Holotype, Io.6246, female left valve (Pl. 14, fig. 10; Text-fig. 22a), length 0·32 mm; height 0·16 mm. Paratypes: Io.6247, male right valve (Pl. 14, fig. 11), length 0·37 mm; height 0·18 mm. Io.6248, male left valve (Pl. 14, fig. 12; Text-fig. 22b), length 0·37 mm; height 0·17 mm. Io.6250, female right valve, length 0·36 mm; height 0·19 mm.

Discussion. The degree of development of the tubercles in *Looneyella africana* sp. nov. is variable in that the most posterior postero-dorsal tubercle may be only very poorly developed. Likewise the tubercle at the posterior end of the ventro-lateral ridge may be variable in its development. In some specimens the ventro-lateral ridge itself may become nodose.

Originally (Bate 1975) this species was assigned to the genus *Orthonotacythere* Alexander 1933, which it closely resembles on carapace outline and tuberculate surface ornamentation. However, *Looneyella* differs from *Orthonotacythere* in the development of a curved, ventro-lateral ridge that tends to turn upwards anteriorly and fuse with the eye node. Closer examination of this East African species confirmed that it should more accurately be placed in *Looneyella*.

L. africana differs from the Cretaceous *L. monticula* (Jones 1893) and the Jurassic *L. subtilis* Oertli 1959 in the more rectangular carapace outline, reticulate shell surface and position of the tubercles.

IV. FAUNAL ASSEMBLAGES

The ostracods described in this paper were obtained from five stratigraphical units (see Table 1), each unit having its own ostracod faunal assemblage and each assemblage characterized by a species of the ostracod genus *Majungaella*. The ostracod faunas are described in ascending stratigraphical order.

Middle Callovian fauna. *Majungaella mundula* (Grekoff) in association with (a) in the Wami River Area: *Paracypris* sp. B, *Paracypris* aff. *contermia*, *Cytherella masuguluensis*, *Cytherella* cf. *collapsa*, *Pirileberis prognata*, *Amicytheridea ihopyensis* and *Afrocytheridea laevigata*. (b) in the Mandawa Anticline: *Cytherella knysnaensis*, *Cytherelloidea brentonensis*, *Amicytheridea ihopyensis*, *Amicytheridea triangulata*, *Afrocytheridea faveolata*, '*Cytheretta*' sp., *Darwinula* sp., *Bairdia* sp. C, *Asciocythere* sp., *Procytheridea disparlateralis*, *Procytherura* sp., *Monoceratina* sp. B and *Eucytherura* sp.

The two ostracod assemblages listed above come from Middle Callovian sediments dated on ammonite evidence as belonging to the *anceps* Zone. They are, therefore, of the same age. Within the time span of an ammonite zone it is possible that more than a single ostracod fauna developed. Here the two assemblages are linked by the common ostracods *Majungaella mundula* and *Amicytheridea ihopyensis*, but it is probably significant that the two assemblages are not only widely separated geographically but that the southern fauna contains evidence, the presence of charophytes and of the ostracod *Darwinula* sp., of the closeness of land and the influx of fresh water. Thus the differences in faunas could be attributed either to differing environmental conditions, the northern fauna being the more truly marine, or to slight differences in stratigraphical position.

TABLE 1

Range table of Callovian to Tithonian Ostracoda from Tanzania

CALLOVIAN					OXFORDIAN				L. KIMMERIDGIAN				M. or Up KIMMERIDGIAN			TITHONIAN			STAGE
Mandawa Anticline			Wami River		Wami River				Mandawa Anticline										REGION
B 114	B 97	B 92	B 66	BM 94	B 2	BM 86	B 67	B 68	B 103a	B 104a	B 106a	B 107a	B 219	B 222	B 223	B 105b	B 110	B 111	SAMPLE
																	●	●	*Pirileberis?* sp.
			●														●	●	*Pireleberis prognata* Grekoff
																●	●	●	*Majungaella perforata* Grekoff
																●			*Cytherella* sp.
													●	●	●				*Majungaella praeperforata* Bate
									●				●	●	●				*Procytherura aerodynamica* Bate
						●		●				●	●		●				*Tricordis triangula* Bate
										●		●	●		●				*Cytheropteron aitkeni* Bate
													●		●				*Cytherella mandawaensis* Bate
													●		●				*Paracypris* sp. A
													●		●				*Monoceratina* sp. A
													●						*Mandelstamia* sp.
													●						*Bythocypris* sp. A
													●		●				*Mandelstamia grekoffi* Bate
													●		●				*Cytheropteron ndaui* Bate
															●				*Pleurocythere tanzanensis* Bate
													●		●				*Bairdia* sp. A
													●		●				*Pontocyprella* sp.
													●		●				*Rhadinocythere gracilis* Bate
													●		●				*Fastigatocythere* aff. *brentonensis* (Dingle)
													●		●				*Looneyella africana* Bate
													●		●				*Acrocythere ? tricostata* Bate
													●		●				*Paracytheridea mandawaensis* Bate
													●		●				*Mandawacythere striata* Bate
															●				*Cytheropteron* sp
												●	●						*Cytherelloidea* sp.
									●	●	●	●							*Galliaecytheridea manyuliensis* Bate
									●	●	●								*Majungaella kimmeridgiana* Bate
					●			●											*Bairdia* sp. B
						●	●	●											*Cytherella umbilica* Bate
						●	●	●											*Bythocypris* sp. B
					●		●												*Majungaella oxfordiana* Bate
					●	●	●												*Cytheropteron grekoffi* Bate
				●	●														*Paracypris* sp. B
			●	●															*Cytherella masuguluensis* Bate
●	●	●																	*Cytherella knysnaensis* Dingle
●	●			●															*Amicytheridea ihopyensis* (Grekoff)
			●																*Cytherella* cf. *collapsa* Grekoff
			●																*Paracypris* aff. *contermia* Ljubimova & Mohan
	●		●																*Majungaella mundula* (Grekoff)
			●																*Afrocytheridea laevigata* Bate
●																			*"Cytheretta"* sp.
●																			*Darwinula* sp.
●	●																		*Afrocytheridea faveolata* Bate
●	●																		*Bairdia* sp. C
●																			*Asciocythere ?* sp
	●																		*Procytheridea disparlateralis* Bate
	●																		*Amicytheridea triangulata* Bate
	●																		*Procytherura* sp
	●																		*Monoceratina* sp. B
	●																		*Eucytherura* sp.
	●																		*Cytherelloidea brentonensis* Dingle

UPPER OXFORDIAN FAUNA. *Majungaella oxfordiana* with *Paracypris* sp. B, *Cytheropteron grekoffi*, *Bythocypris* sp. B, *Cytherella umbilica*, *Bairdia* sp. B and *Trichordis triangula*. The richness of the Upper Oxfordian fauna is possibly limited by the arenaceous facies which has tended to facilitate removal of the microfossils by solution. The size of the fauna is not considered to be a true reflection on the size of the living ostracod populations.

LOWER KIMMERIDGIAN FAUNA. *Majungaella kimmeridgiana* with *Procytherura aerodynamica*, *Cytheropteron* (? *Infracytheropteron*) *aitkeni*, *Trichordis triangula*, *Galliaecytheridea manyuliensis* and *Cytherelloidea* sp. Again a rather poor fauna in terms of number of species but excessively rich in number of individuals. The three dominant species are *Majungaella kimmeridgiana*, *Galliaecytheridea manyuliensis* and *Procytherura aerodynamica*.

Possible reasons for the reduction in the number of species accompanied by an increase in the number of individuals cannot be the same as given for the reduced Oxfordian fauna. A reduction in the number of species is often associated with a change in the salinity from normal marine to either euryhaline or to hyperhaline conditions. In both cases a numerical increase in the number of individuals often follows. The presence of ammonites in the succession, however, suggests that normal marine conditions prevailed. Perhaps the reason for the reduced fauna lies in a lowering of the water temperature, but it is not possible on the evidence available to be more conclusive on this matter at the present time.

MIDDLE OR UPPER KIMMERIDGIAN FAUNA. *Majungaella praeperforata* with *Procytherura aerodynamica*, *Trichordis triangula*, *Cytheropteron* (? *Infracytheropteron*) *aitkeni*, *Cytheropteron* (*I.*) *ndaui*, *Cytheropteron* sp., *Cytherella mandawaensis*, *Cytherelloidea* sp., *Paracypris* sp. A, *Monoceratina* sp. A, *Mandelstamia* sp., *Mandelstamia grekoffi*, *Bythocypris* sp. A, *Pleurocythere tanzanensis*, *Bairdia* sp. A, *Pontocyprella* sp., *Rhadinocythere gracilis*, *Fastigatocythere* aff. *brentonensis*, *Looneyella africana*, *Acrocythere* ? *tricostata*, *Paracytheridea mandawaensis* and *Mandawacythere striata*. This is a typical marine continental shelf fauna rich in both species and in individuals. The presence of *Procytherura aerodynamica* sp. nov. off Western Australia (as Indet. sp. E of Oertli 1974), indicates that a stratigraphical correlation between East Africa and Australia should be possible.

TITHONIAN FAUNA. *Majungaella perforata* with *Pirileberis prognata*, *Pirileberis* ? sp. and *Cytherella* sp. Although the Tithonian samples may be subdivided into (?) Lower Tithonian (sample B105b) and Upper Tithonian (samples B110 and B111) the fauna is so small that it is preferable to consider it as a single assemblage. Preservation is not good and, as in the Oxfordian, extensive decalcification has taken place.

Only one ostracod genus, *Majungaella*, stands out as a useful marker fossil, the five species of which each characterize a broad stratigraphical unit. As such they are of considerable importance in correlating the Jurassic of East Africa with that of India and Madagascar – although all five species have not yet been identified from all three regions. Nevertheless the fact that the earliest and the last species of the five are known from all three regions points to the likelihood that the presence of the other three may be discovered eventually.

The majority of the species described from Tanzania have a restricted vertical range and fall conveniently into five faunal assemblages. Of the 52 species recorded only six, *Cytherelloidea* sp., *Cytheropteron* (*?I.*) *aitkeni* Bate, *Pirileberis prognata* Grekoff, *Trichordis triangula* Bate and *Procytherura aerodynamica* Bate, occur in more than one faunal assemblage.

V. CORRELATION

Because of the paucity of exposures within Tanzania the sequence of Callovian to Tithonian has only been observed in relatively few outcrops and thus correlation between different sections has generally not been possible. The Middle Callovian (*anceps* Zone) is the only unit found in both the Wami River Area and the Mandawa Anticline that has yielded a microfossil assemblage. The Oxfordian of the Mandawa Anticline proved to be barren and the Kimmeridgian–Tithonian is not present in the Wami River Area.

Although the Middle Callovian fauna from the Mandawa Anticline differs from that of the Wami River, for reasons already discussed (p. 214), the presence of *Majungaella mundula* (Grekoff) and *Amicytheridea ihopyensis* (Grekoff) in both provides some means of correlation.

Fifty-two ostracod species are recorded here from the Callovian to Tithonian of Tanzania and this compares with the 49 species described by Grekoff (1963) from the Bajocian to Valanginian of Madagascar. Guha (1975 ?) records 40 species from the Bathonian to Valanginian of Kutch, and Dingle (1972) describes eight species from sediments considered to be Callovian from South Africa. This is the total available information at the present time on the Jurassic ostracod fauna of the countries bordering the Indian Ocean.

Correlation between the Middle Callovian of Tanzania and the supposed Callovian of South Africa is rather tenuous, only two species being common to both regions, *Cytherella knysnaensis* Dingle and *Cytherelloidea brentonensis* Dingle. One species, *Fastigatocythere* aff. *brentonensis* Dingle, has affinities with the species of that name from South Africa but the absence from the South African Callovian of a species of *Majungaella* makes a precise correlation impossible.

Eight species are common to Tanzania and Madagascar as follows. Callovian, *Amicytheridea ihopyensis* (Grekoff), *Majungaella mundula* (Grekoff) and *Afrocytheridea faveolata* Bate. Middle or Upper Kimmeridgian, *Amicytheridea triangulata* Bate and *Mandawacythere striata* Bate. Tithonian, *Pirileberis prognata* Grekoff and *Majungaella perforata* Grekoff. *Cytheropteron grekoffi* Bate (= *Cytheropteron* 1040 of Grekoff) is found in the Oxfordian of Tanzania and in the Kimmeridgian to Portlandian of Madagascar.

Five ostracods are common to Tanzania and Kutch. Callovian, *Amicytheridea ihopyensis* (Grekoff) and *Majungaella mundula* (Grekoff). Middle or Upper Kimmeridgian, *Mandawacythere striata* Bate. Tithonian, *Pirileberis prognata* Grekoff and *Majungaella perforata* Grekoff.

A much larger number of ostracods (14 species) is common to Kutch and Madagascar, which might indicate a closer relationship between these two countries than exists between either and Tanzania. More probably the difference is the result of incomplete sampling and of weathering. It is expected that future studies will confirm this by increasing the number of known ostracod species common to all three countries. East to the West Australian continental shelf, core 30 of site 263 (Oertli 1974) has revealed the presence of *Procytherura aerodynamica* (as Indet. sp. E). This suggests that a stratigraphical correlation for the Jurassic between East Africa and Western Australia will be possible.

VI. CONCLUSIONS

The Callovian to Tithonian sediments examined in this study represent a marine, shallow water continental shelf environment. The closeness of land nearby is confirmed at one horizon in the Middle Callovian of the Mandawa Anticline by the presence, within the microfossil assemblage, of charophytes and freshwater ostracods.

Five ostracod faunal assemblages, each characterized by a species of *Majungaella*, have been recognized. Although the importance of *Majungaella* species has not been fully tested, the evidence so far – the occurrence of *M. mundula* (Grekoff) in both north and south Tanzania, India and Madagascar and of *M. perforata* Grekoff in Tanzania, India and Madagascar – already indicates the value of this genus in regional correlation. The faunal assemblages themselves have not yet been used in correlation but the potential exists, with more detailed sampling, for a more precise comparison of the Jurassic not only of East Africa, Madagascar and India, but between all countries bordering the Indian Ocean having marine Jurassic sediments.

The Jurassic ostracods of Tanzania, Madagascar and India represent what is termed here a 'southern fauna', although perhaps a more precise term would be that of a 'south of the Tethys' fauna. The northern hemisphere position of India today is anomalous ; we must take into account that it was located further south during Jurassic times when the regions of deposition were very much closer than they are at the present day.

Although many genera of the southern fauna have a cosmopolitan distribution (e.g. *Cytherella*, *Cytherelloidea*, *Bairdia*, *Cytheropteron* and *Paracypris*), many are known only from the area south of the Tethys (*Majungaella*, *Trichordis*, *Amicytheridea*, *Pirileberis*, *Afrocytheridea*, *Rhadinocythere* and *Mandawacythere*). Of these, *Majungaella* is of interest because of its phylogenetic relationship to the northern genus *Progonocythere* Sylvester-Bradley 1948, which, apart from one known species (*P. laeviscula* Ljubimova & Mohan 1960), it replaces completely in the Jurassic succession.

One ostracod, *Pleurocythere tanzanensis* Bate, although considered to belong to the northern genus *Pleurocythere*, has significant morphological differences that establish it as a southern form which has undergone evolutionary change since its migration south.

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PLATE 1

Cytherella knysnaensis Dingle (p. 172)
Middle Callovian, sample B97

FIG. 1. Left side, complete carapace, Io.6021, ×70.
FIG. 5. Dorsal view, complete carapace, Io.6022, ×70.

Cytherella masuguluensis sp. nov. (p. 173)
Middle Callovian, sample B66

FIG. 2. Left side, complete carapace, holotype, Io.6029, ×70.
FIG. 10. Dorsal view, complete carapace, paratype, Io.6030, ×70.

Cytherella mandawaensis sp. nov. (p. 172)
Middle or Upper Kimmeridgian

FIG. 3. Left side, complete carapace, holotype Io.6023, sample B223, ×70.
FIG. 4. Internal view, right valve, paratype Io.6027, sample B219, ×70.
FIG. 7. External view, right valve, paratype Io.6026, sample B219, ×70.
FIG. 8. External view, left valve, paratype Io.6025 sample B219, ×70.
FIG. 9. Dorsal view, complete carapace, paratype Io.6028, sample B223, ×70.

Cytherella sp. (p. 174)

FIG. 6. (?) Lower Tithonian, sample B105b. External view, left valve, Io.6036, ×68.

Cytherella cf. ***collapsa*** Grekoff (p. 171)

FIG. 11. Middle Callovian, sample B66. External view, left valve, Io.5821, ×90.

Cytherella umbilica sp. nov. (p. 173)
Upper Oxfordian, sample B67.

FIG. 12. External view, left valve, paratype Io.6033 ×59.
FIG. 13. External view, right valve, holotype Io.6032 ×48.
FIG. 14. External view, right valve, paratype Io.6034 ×74.

Cytherelloidea sp. (p. 174)

FIG. 15. Lower Kimmeridgian, sample B107a. External view, left valve, Io.6039, ×70.

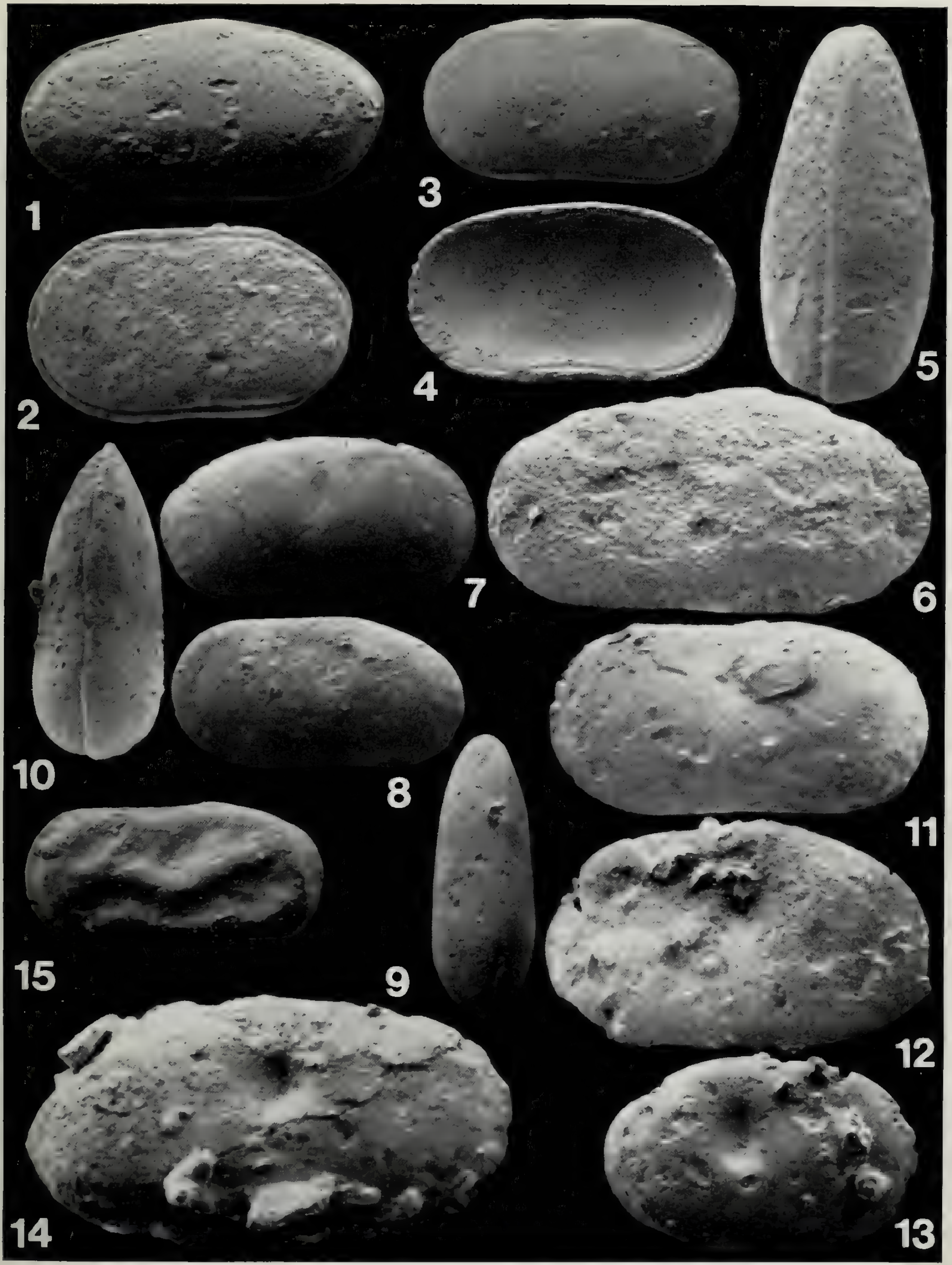
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PLATE 2

Cytherelloidea brentonensis Dingle (p. 174)

FIG. 1. Middle Callovian, sample B97. External view, left side, complete carapace, Io.6037, ×50.

Paracypris sp. B (p. 178)

FIG. 2. Middle Callovian, sample BM94. External view, left side, complete carapace, Io.6050, ×80.

Monoceratina sp. B (p. 180)

FIG. 3. Middle Callovian, sample B97. External view, left valve, Io.6059, ×100.

Paracypris sp. A (p. 178)

Middle or Upper Kimmeridgian, sample B223

FIG. 4. External view, left side, complete carapace, Io.6049, ×70.

FIG. 5. External view, right side, complete carapace, Io.6048, ×70.

Paracypris aff. **P. contermia** Ljubimova & Mohan (p. 177)

FIG. 6. Middle Callovian, sample B66. External view, right side, complete carapace, Io.6047, ×80.

Bythocypris sp. B (p. 177)

FIG. 7. Upper Oxfordian, sample B67. External view, right side, complete carapace, Io.6045, ×70.

Bythocypris sp. A (p. 176)

FIG. 8. Middle or Upper Kimmeridgian, sample B219. External view, left valve, Io.6044, ×70.

Bairdia sp. C (p. 175)

Middle Callovian

FIG. 9. External view, right side, juvenile carapace, Io.6043, sample B114, ×100.

FIG. 13. External view, right side, adult carapace, Io.6042, sample B97, ×90.

Monoceratina sp. A (p. 179)

Middle or Upper Kimmeridgian, sample B219

FIG. 10. External view, right side, complete carapace, Io.6057, ×70.

FIG. 11. External view, left side, complete carapace, Io.6058, ×70.

Darwinula sp. (p. 179)

FIG. 12. Middle Callovian, sample B114. External view, right side, complete carapace, Io.6056, ×70.

Bairdia sp. A (p. 175)

FIG. 14. Middle or Upper Kimmeridgian, sample B223. External view, right side, juvenile carapace, Io.6040, ×129.

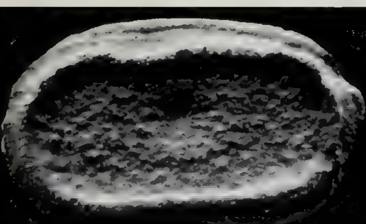
Pontocyprella sp. (p. 178)

Middle or Upper Kimmeridgian, sample B223

FIG. 15. Internal view, right valve, Io.6054, ×120.

FIG. 16. External view, left valve, Io.6051, ×120.

FIG. 17. External view, right side, complete carapace, Io.6053, ×120.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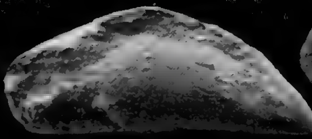
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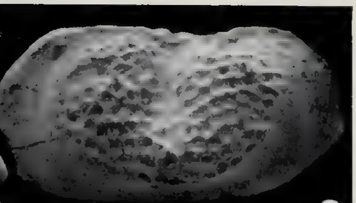
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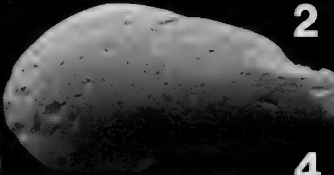
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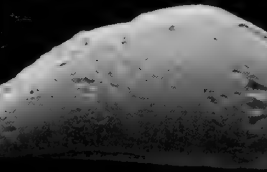
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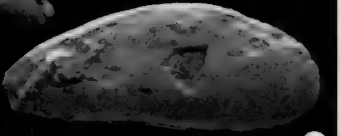
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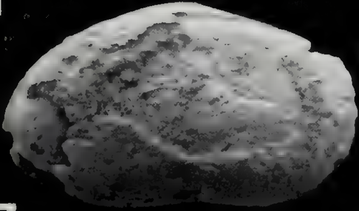
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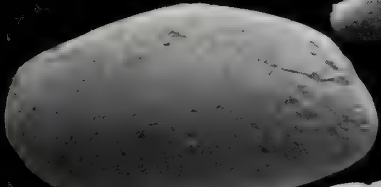
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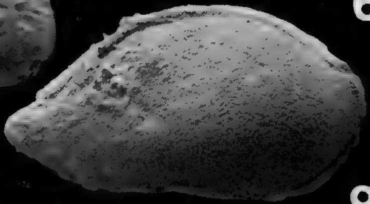
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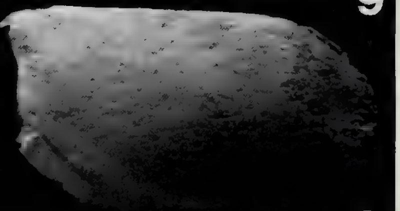
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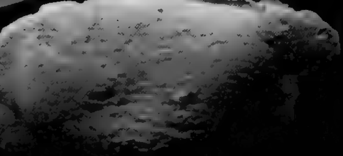
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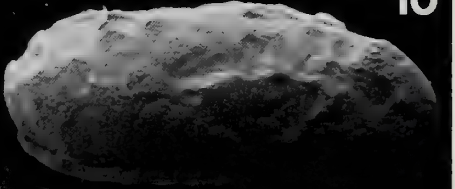
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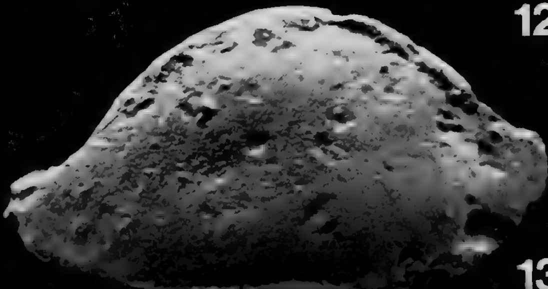
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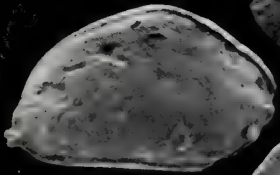
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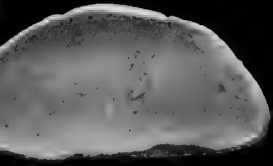
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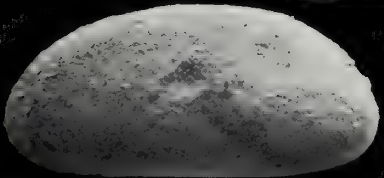
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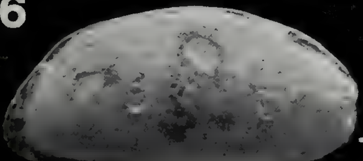
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PLATE 3

Majungaella perforata Grekoff (p. 181)
Tithonian

FIG. 1. External view, left side, male carapace, Io.6065, sample B111, × 80.

FIG. 2. External view, left side, female carapace, Io.6064, sample B111, × 80.

FIG. 3. External view, right side, male carapace, Io.6063, sample B110, × 80.

FIG. 7. Dorsal view, female carapace, Io.6062, sample B110, × 80.

Majungaella praeperforata sp. nov. (p. 182, see also Pl. 4, figs 1–3)
Middle or Upper Kimmeridgian, sample B219

FIG. 4. External view, female left valve, paratype Io.6067, × 70.

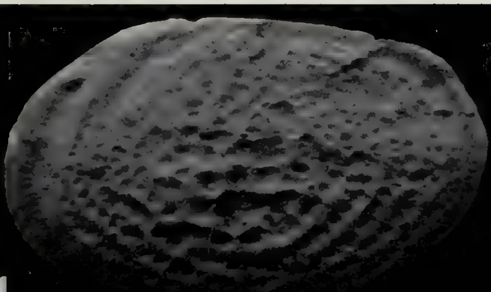
FIG. 5. External view, male left valve, paratype Io.6068, × 70.

FIG. 6. External view, right side, female carapace, holotype Io.6066, × 70.

FIG. 8. Internal view, female left valve, paratype Io.6072, × 70.

FIG. 9. Internal view, female right valve, paratype Io.6070, × 70.

FIG. 10. Anterior duplicature showing marginal pore canals, male right valve, paratype Io.6069, × 180.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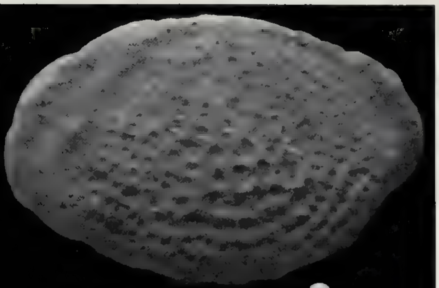
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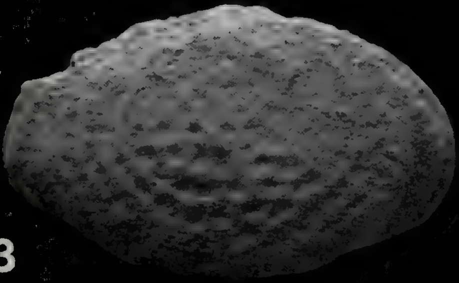
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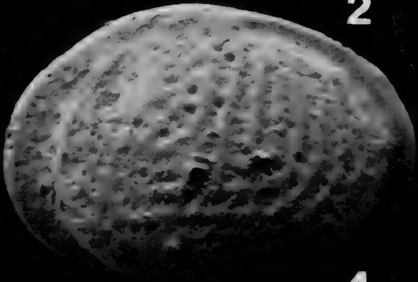
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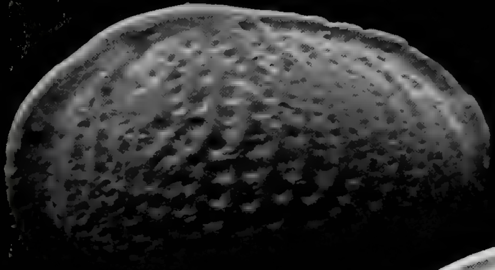
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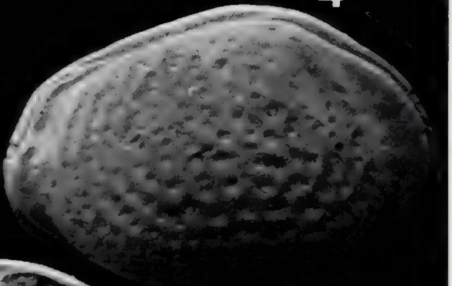
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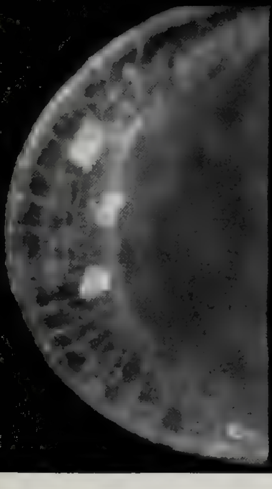
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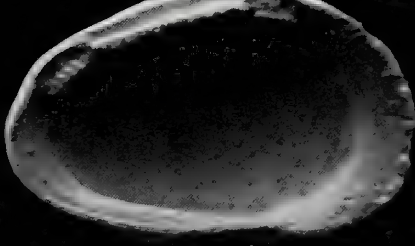
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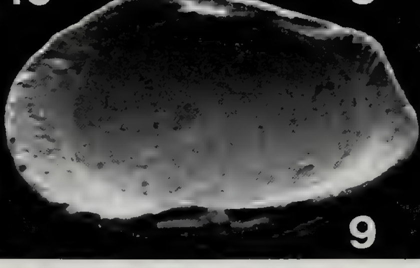
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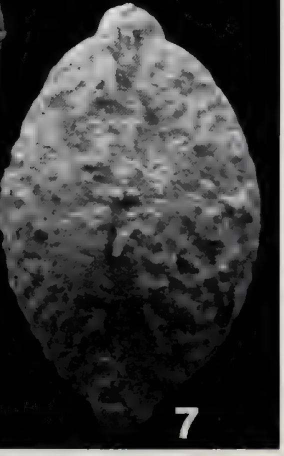
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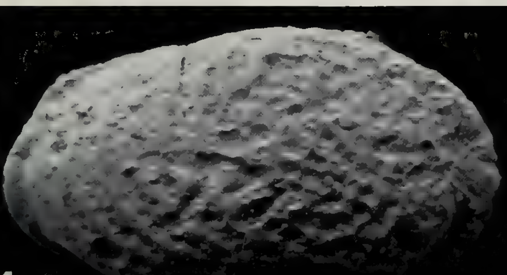
PLATE 4

Majungaella praeperforata sp. nov. (p. 182, see also Pl. 3, figs 4–6, 8–10)
Middle or Upper Kimmeridgian, sample B219

Fig. 1. External view, male right valve, paratype Io.6073, × 70.
Fig. 2. Dorsal view, female carapace, paratype Io.6071, × 70.
Fig. 3. Ventral view, female carapace, paratype Io.6074, × 70.

Majungaella kimmeridgiana sp. nov. (p. 183, see also Pl. 5, figs 1–3)
Lower Kimmeridgian

Fig. 4. External view, right side, female carapace, holotype Io.6075, sample B103a, × 80.
Fig. 5. External view, left side, female carapace, paratype Io.6085, sample B103a, × 80.
Fig. 6. Ventral view, female carapace, paratype Io.6084, sample B103a, × 80.
Fig. 7. Dorsal view, male carapace, paratype Io.6081, sample B104a, × 80.
Fig. 8. Dorsal view, median hinge bar, female left valve, paratype Io.6080, sample B104a, × 250.
Fig. 9. Internal view, female left valve, paratype Io.6077, sample B103a, × 80.
Fig. 10. Dorsal view, female carapace, paratype Io.6086, sample B103a, × 80.
Fig. 11. Right valve hinge, female paratype Io.6078, sample B103a, × 170.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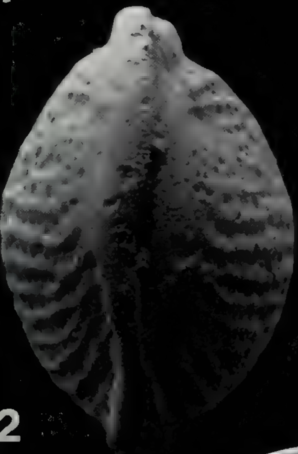
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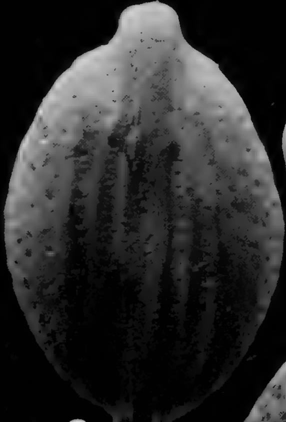
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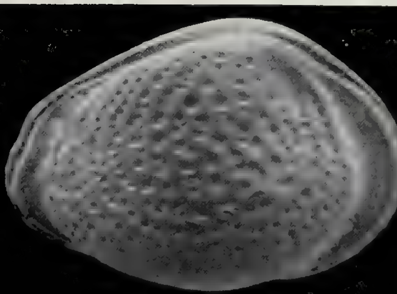
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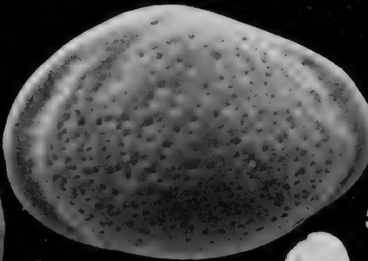
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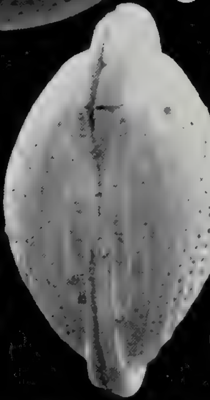
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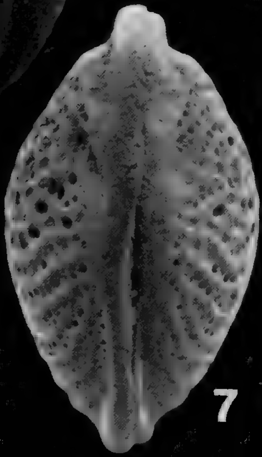
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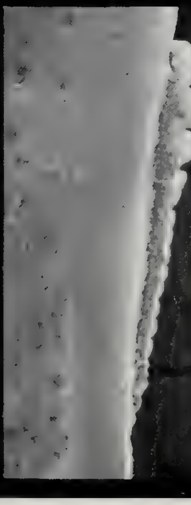
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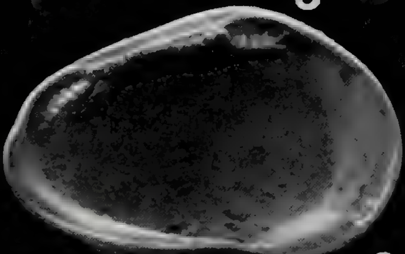
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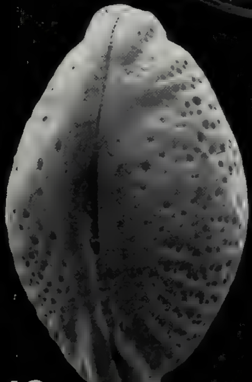
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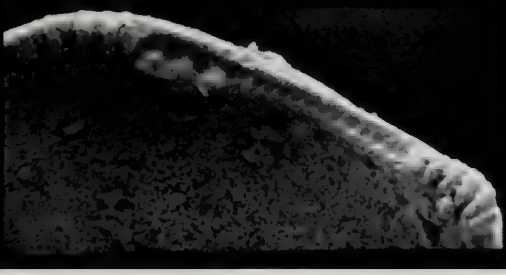
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PLATE 5

Majungaella kimmeridgiana sp. nov. (p. 183, see also Pl. 4, figs 4–11)
Lower Kimmeridgian

FIG. 1. External view, right side, male carapace, paratype Io.6076, sample B103a, × 80.

FIG. 2. External view, male left valve, paratype Io.6083, sample B103a, × 80.

FIG. 3. Ventral view, male carapace, paratype Io.6082, sample B104a, × 80.

Majungaella oxfordiana sp. nov. (p. 185)
Upper Oxfordian, sample B2

FIG. 4. External view, right side, male carapace, paratype Io.6089, × 80.

FIG. 5. External view, right side, female carapace, holotype Io.6088, × 80.

FIG. 6. Dorsal view, female carapace, paratype Io.6093, × 80.

FIG. 7. Internal view, female left valve, paratype Io.6092, × 80.

FIG. 8. Dorsal view to show median hinge element, female left valve, paratype Io.6090, × 80.

FIG. 9. External view, female right valve, paratype Io.6091, × 80.

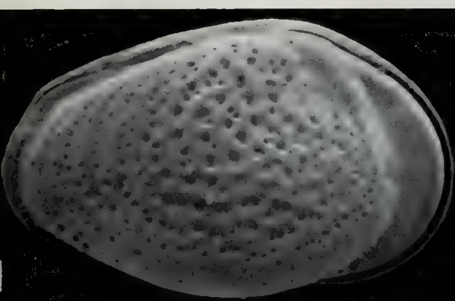
Majungaella mundula (Grekoff) (p. 185)
Middle Callovian, sample B66

FIG. 10. External view, right side, complete carapace, Io.6096, × 90.

FIG. 11. Ventral view, complete carapace, Io.6098, × 90.

FIG. 12. External view, left side, complete carapace, Io.6095, × 90.

FIG. 13. Dorsal view, complete carapace, Io.6097, × 90.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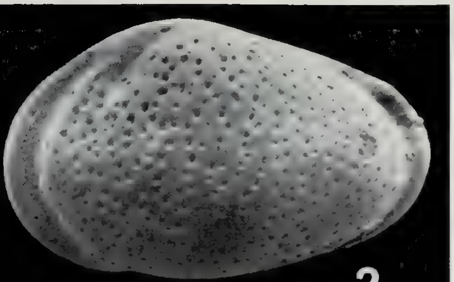
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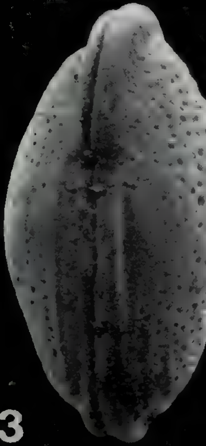
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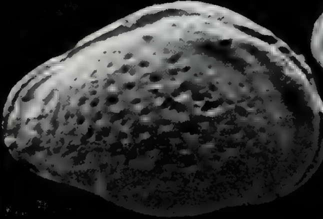
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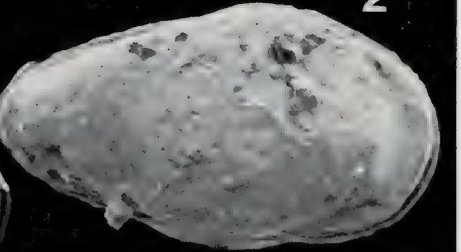
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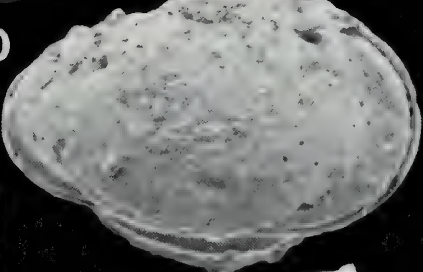
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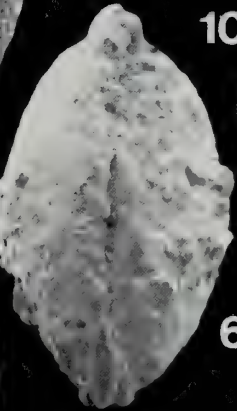
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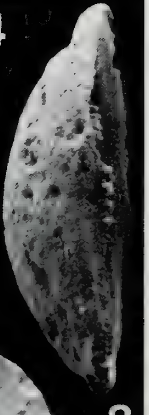
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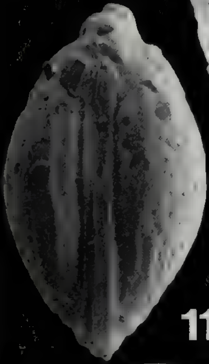
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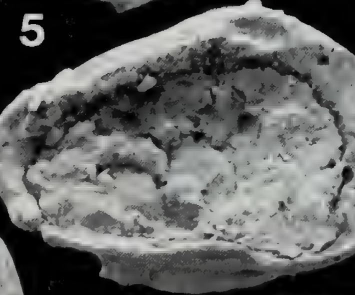
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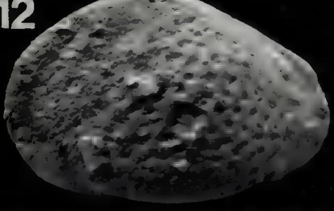
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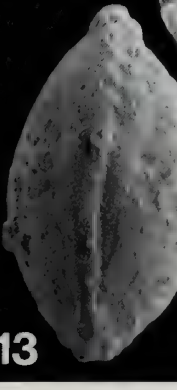
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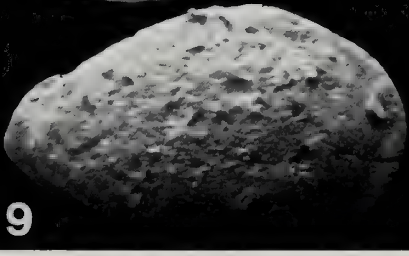
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PLATE 6

Trichordis triangula sp. nov. (p. 187)

Oxfordian, Lower and Middle or Upper Kimmeridgian

FIGS 1, 5. Right side and ventral view, female carapace, holotype Io.6105, sample B219, × 100.

FIG. 2. Internal view, female left valve, paratype Io.6110, sample B219, × 100.

FIG. 3. External view, female left valve, paratype Io.6109, sample B219, × 100.

FIG. 4. External view, male left valve, paratype Io.6107, sample B107a, × 100.

FIG. 6. Dorsal view, female carapace, paratype Io.6108, sample B219, × 100.

FIG. 7. External view, female left valve, paratype Io.6106, sample BM86, × 100.

FIG. 8. Adductor and frontal muscle scars (anterior to right), female left valve, paratype Io.6110, sample B219, × 850.

FIG. 14. Internal view, male right valve, paratype Io.6111, sample B223, × 165.

Fastigatocythere aff. **brentonensis** (Dingle) (p. 186, see also Pl. 7, fig. 9)

Middle or Upper Kimmeridgian, sample B223

FIG. 9. External view, left valve showing oblique ribbing, Io.6102, × 120.

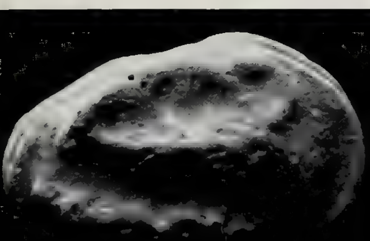
FIG. 10. External view of left valve showing absence of oblique lateral ribbing, Io.6104, × 120.

Pleurocythere tanzanensis sp. nov. (p. 189)

Middle or Upper Kimmeridgian, sample B223

FIGS 11, 12. External views, right and left, complete carapace, holotype Io.6137, × 100.

FIG. 13. External view, broken left valve, paratype Io.6138, × 100.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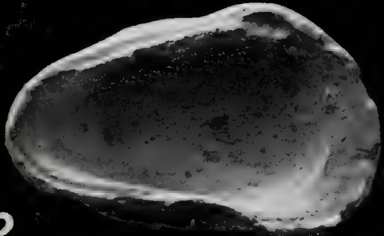
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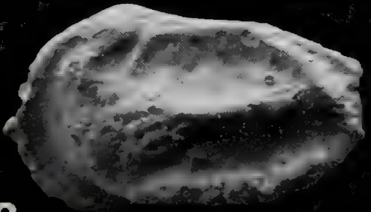
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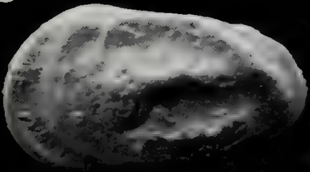
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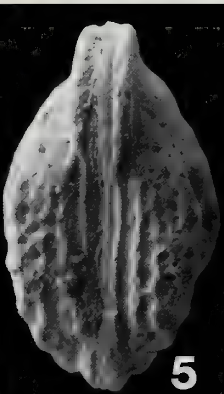
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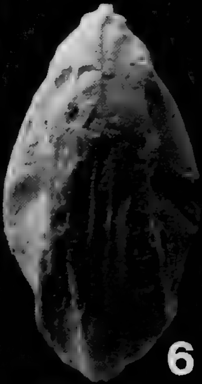
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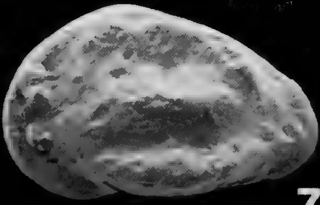
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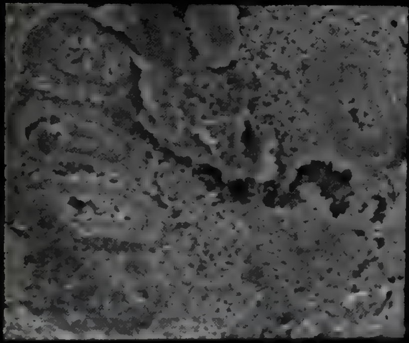
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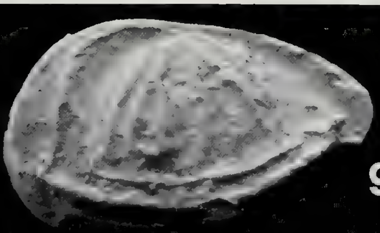
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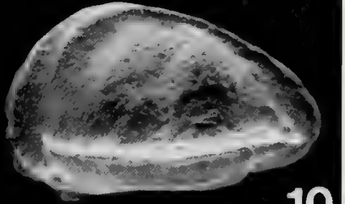
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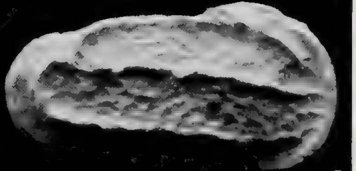
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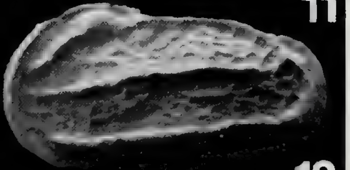
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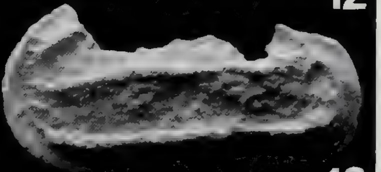
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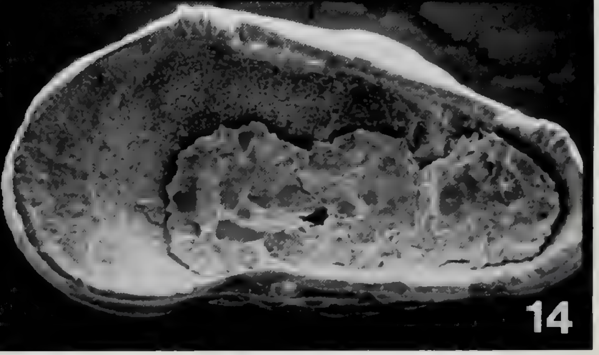
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PLATE 7

Mandelstamia grekoffi sp. nov. (p. 188)

Middle or Upper Kimmeridgian

Fig. 1. Dorsal view, complete carapace, paratype Io.6171, sample B223, × 100.

Fig. 2. External view, complete carapace, paratype Io.6169, sample B219, × 100.

Fig. 3. External view, left valve, paratype Io.6168, sample B219, × 100.

Fig. 4. External view, right valve, holotype Io.6172, sample B219, × 100.

Figs 5, 6. Internal view, × 100 and enlarged view of posterior hinge element, × 290, right valve, paratype Io.6170, sample B223.

Mandelstamia sp. (p. 189)

Middle or Upper Kimmeridgian, sample B223

Fig. 7. External view, left side, complete carapace, Io.6166, × 100.

Fig. 8. External view, right valve, Io.6165, × 100.

Fastigatocythere aff. **brentonensis** (Dingle) (p. 186, see also Pl. 6, figs 9–10)

Fig. 9. Middle or Upper Kimmeridgian, sample B223. Dorsal view, left valve, Io.6103, × 120.

Amicytheridea ihopyensis (Grekoff) (p. 191)

Middle Callovian

Fig. 10. Internal view, female left valve, Io. 6117, sample B97, × 90.

Fig. 11. External view, right side, female carapace, Io.6251, sample B97, × 90.

Fig. 12. External view, female carapace, Io.6118, sample BM94, × 90.

Fig. 13. Dorsal view, female carapace, Io.6119, sample B97, × 90.

Amicytheridea triangulata sp. nov. (p. 192)

Middle Callovian, sample B97

Figs 14, 15. Dorsal and right views, male carapace, paratype Io.6113, × 80.

Fig. 16. External view, female left valve, holotype Io.6114, × 80.

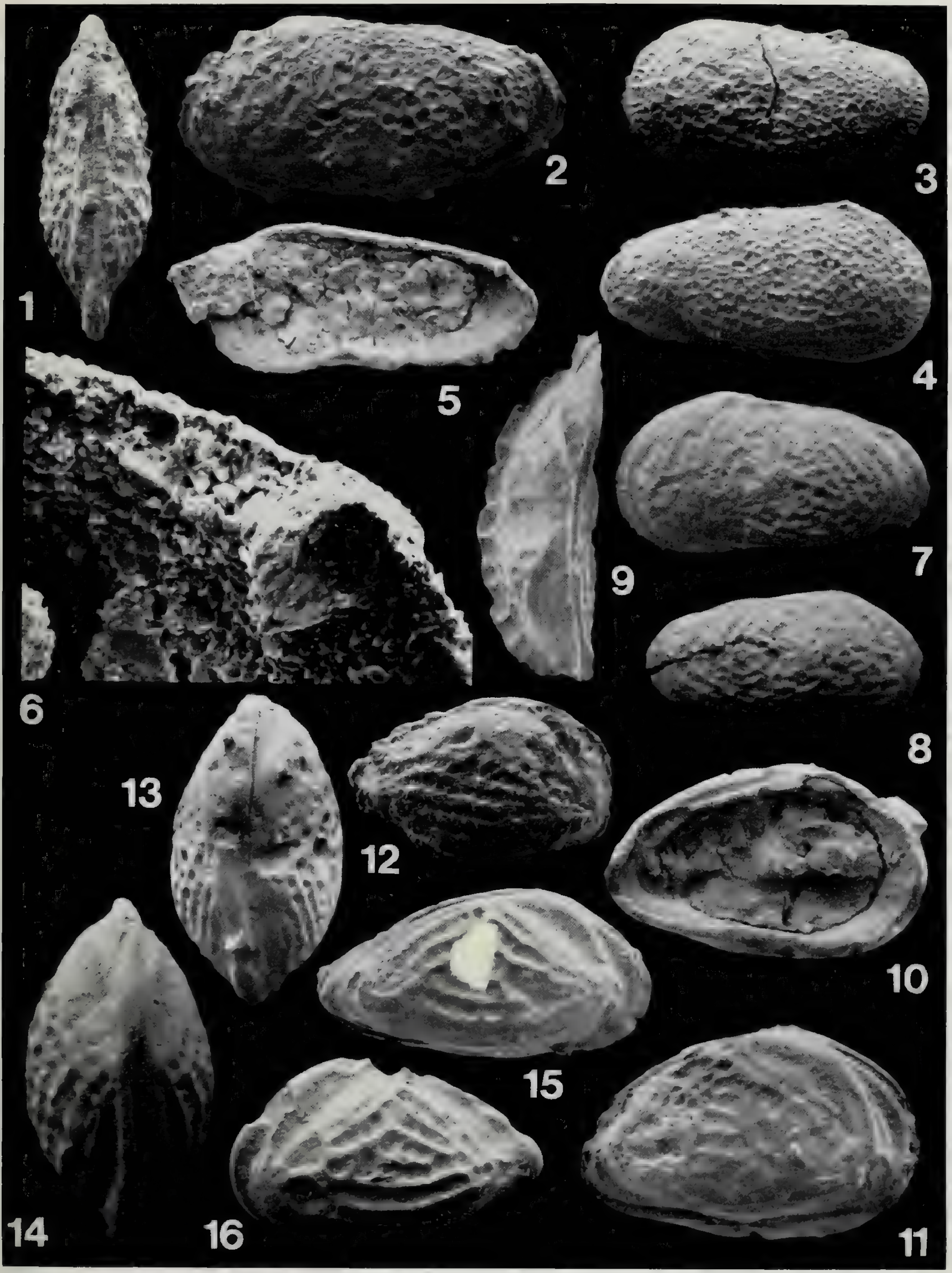
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PLATE 8

Asciocythere ? sp. (p. 193)
Middle Callovian, sample B114

FIG. 1. External view, left side, complete carapace, Io.6253, ×150.
FIG. 2. External view, right side, complete carapace, Io.6252, ×150.

Pirileberis ? sp. (p. 194)
Tithonian

FIG. 3. Dorsal view, complete carapace, Io.6162, sample B110, ×90.
FIG. 4. Internal view, left valve, Io.6159, sample B110, ×90.
FIG. 5. External view, left side, complete carapace, Io.6160, sample B111, ×90.
FIG. 6. External view, right side, complete carapace, Io.6158, sample B111, ×90.

Procytheridea disparlateralis sp. nov. (p. 199)
Middle Callovian, sample B97

FIG. 7. External view, left side, complete carapace, holotype Io.6135, ×120.
FIG. 8. External view, right side, complete carapace, paratype Io.6134, ×120.

Pirileberis prognata Grekoff (p. 194)
Middle Callovian and Middle or Upper Kimmeridgian

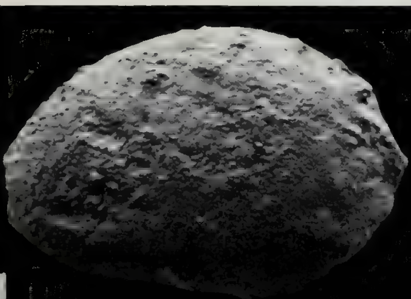
FIG. 9. External view, left side, female carapace, Io.6164, sample B66, ×80.
FIG. 10. External view, right side, male carapace, Io.6154, sample B111, ×70.
FIG. 11. External view, left side, male carapace, Io.6163, sample B66, ×80.

Afrocytheridea faveolata sp. nov. (p. 196)
Middle Callovian, sample B97

FIG. 12. External view, female right valve, holotype Io.6132, ×70.
FIG. 13. External view, male right valve, paratype Io.6128, ×70.

Afrocytheridea laevigata sp. nov. (p. 195, see also Pl. 9, figs 1–4)

FIG. 14. Middle Callovian, sample B66. External view, right side, male carapace, paratype Io.6125, ×70.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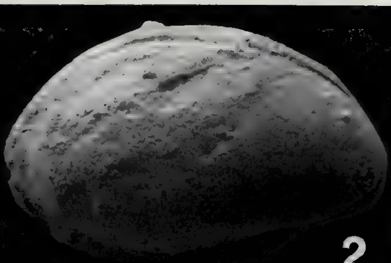
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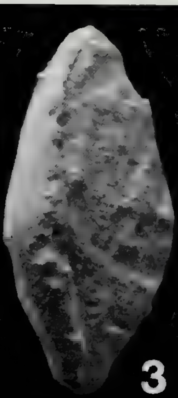
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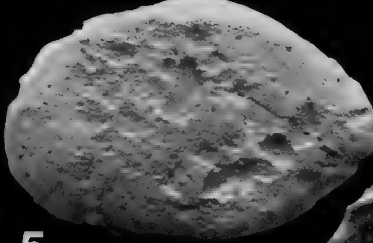
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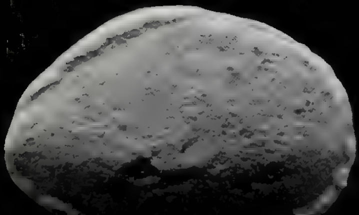
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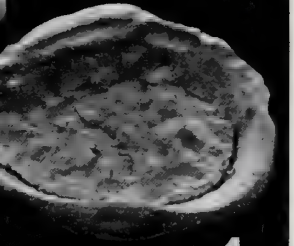
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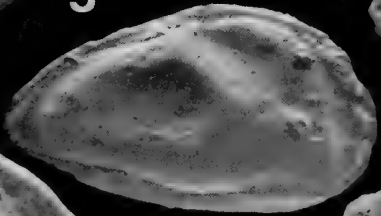
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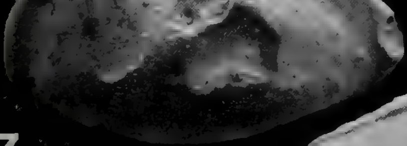
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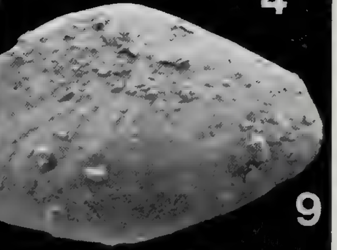
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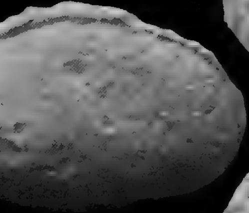
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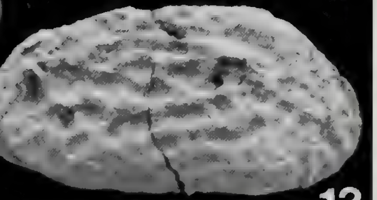
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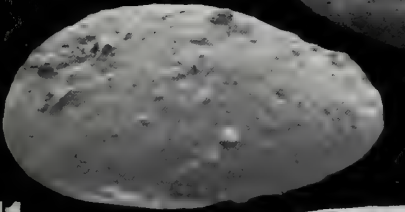
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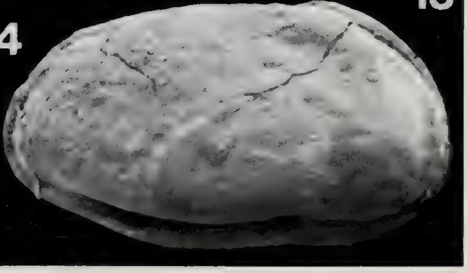
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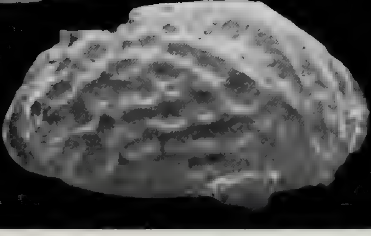
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PLATE 9

Afrocytheridea laevigata sp. nov. (p. 195, see also Pl. 8, fig. 14)
Middle Callovian, sample B66

FIG. 1. External view, left side, female carapace, paratype Io.6123, × 70.

FIG. 2. External view, left side, male carapace, Io.6124, × 70.

FIG. 3. External view, right side, female carapace, Io.6122, × 70.

FIG. 4. Dorsal view, female carapace, paratype Io.6127, × 70.

Galliaecytheridea manyuliensis sp. nov. (p. 197)
Lower Kimmeridgian, sample B107a

FIG. 5. External view, female right valve showing marginal denticles, holotype Io.6141, × 80.

FIG. 6. External view, male left valve, paratype Io.6148, × 80.

FIGS 7, 13. Internal view, × 80 and enlargement of hinge, × 200, female right valve, paratype Io.6143.

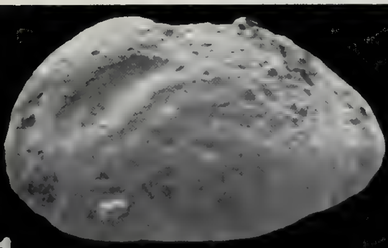
FIG. 8. External view, female left valve, paratype Io.6147, × 80.

FIG. 9. External view, male right valve, paratype Io.6146, × 80.

FIG. 10. Dorsal view to show terminal hinge teeth, female right valve, paratype Io.6144, × 80.

FIGS 11, 14. Enlargement of hinge, × 175, and of muscle scars (anterior to right), × 400, male left valve, paratype Io.6145.

FIG. 12. Enlargement of hinge, female left valve, paratype Io.6142, × 160.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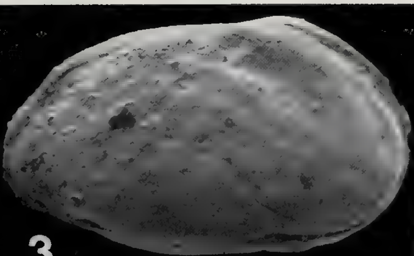
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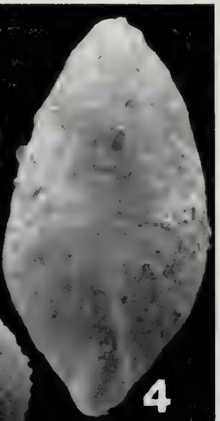
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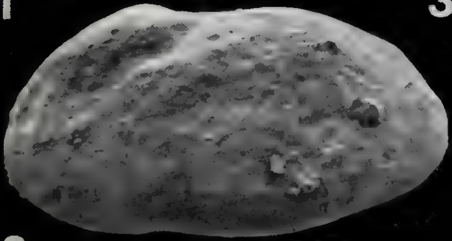
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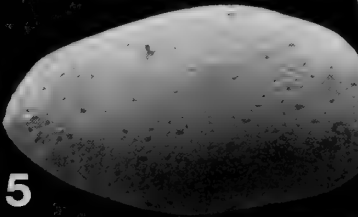
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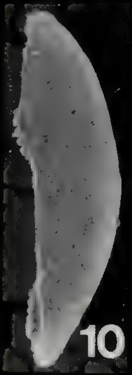
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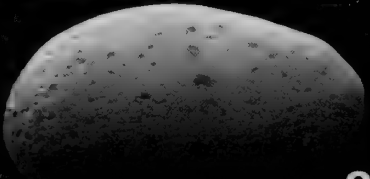
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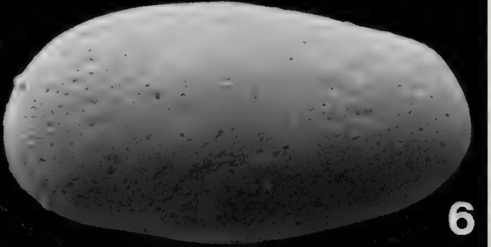
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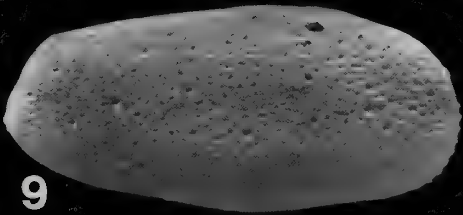
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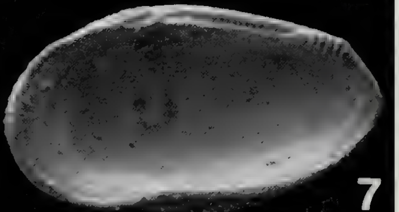
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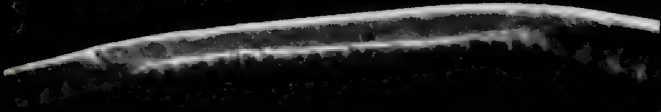
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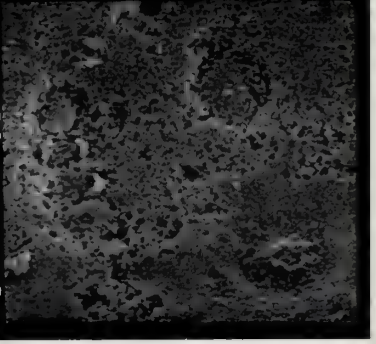
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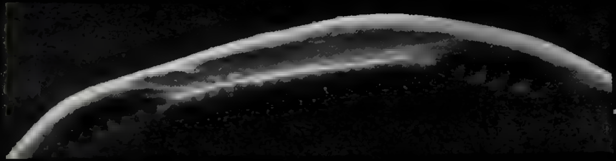
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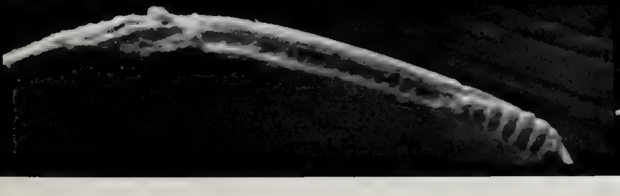
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PLATE 10

'Cytheretta' sp. (p. 200)

FIGS 1, 2. Middle Callovian, sample B114. External views, left and right of complete carapace, Io.6173, × 100.

Mandawacythere striata sp. nov. (p. 201)

Middle or Upper Kimmeridgian

FIGS 3, 4, 10. External and internal views × 150 and muscle scars (anterior to right), × 980, female right valve, holotype Io.6174, sample B219.

FIG. 5. Dorsal view, female carapace, paratype Io.6177, sample B223, × 150.

FIG. 6. Ventral view, female carapace, paratype Io.6178, sample B223, × 150.

FIG. 7. External view, juvenile right valve, paratype Io.6176, sample B223, × 150.

FIGS 8, 9. Internal and external views, male right valve, paratype Io.6175, sample B219, × 150.

Rhadinocythere gracilis sp. nov. (p. 202, see also Pl. 11, figs 1–4)

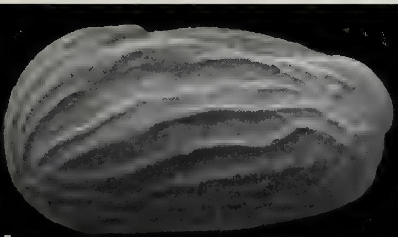
Middle or Upper Kimmeridgian, sample B223

FIG. 11. External view, right side, complete carapace, paratype Io.6184, × 140.

FIG. 12. Internal view, left valve, paratype Io.6186, × 140.

FIG. 13. Internal view, right valve, paratype Io.6185, × 140.

FIG. 14. External view, right side, complete carapace, holotype Io.6182, × 140.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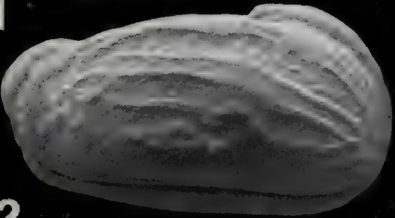
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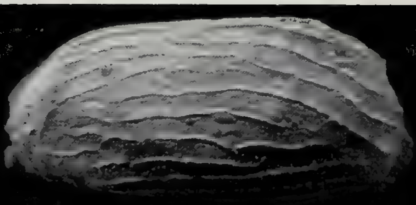
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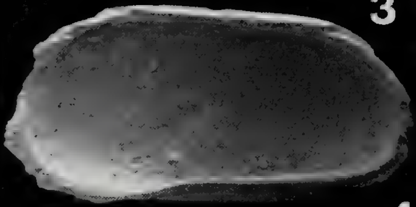
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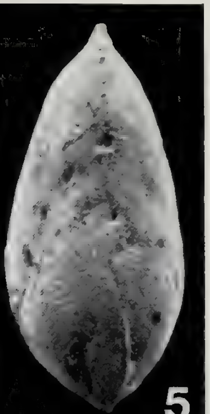
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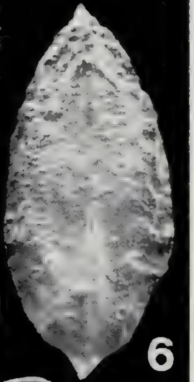
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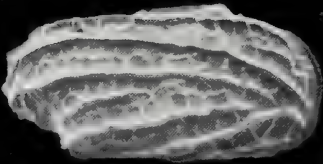
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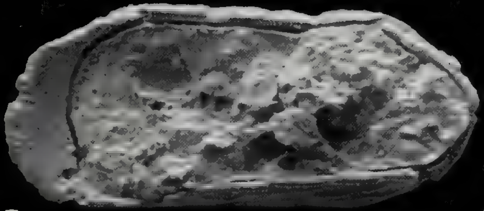
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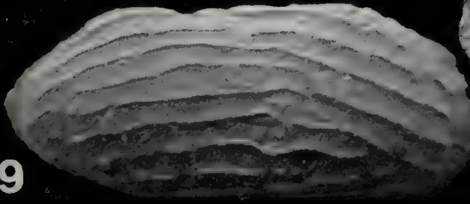
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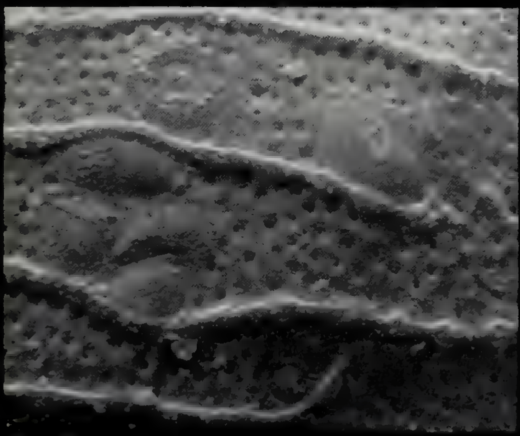
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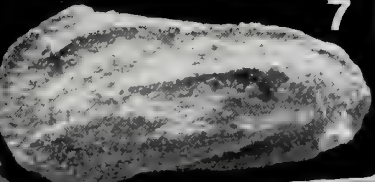
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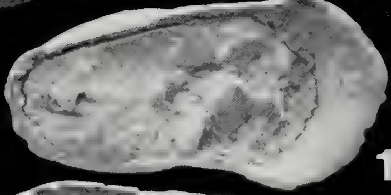
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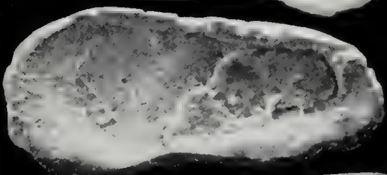
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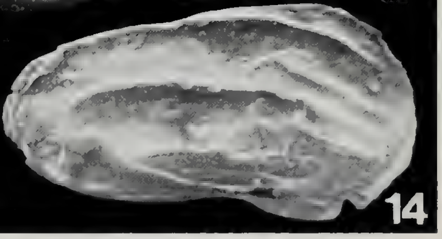
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PLATE 11

Rhadinocythere gracilis sp. nov. (p. 202, see also Pl. 10, figs 11–14)
Middle or Upper Kimmeridgian, sample B223

FIGS 1, 2. Anterior and posterior hinge teeth, right valve, paratype Io.6185, × 1000.

FIGS 3, 4. Dorsal views showing variation in surface ornamentation, paratypes Io.6187 and Io.6183, × 140.

Eucytherura sp. (p. 204)

FIGS 5, 6. Middle Callovian, sample B97. External and internal views, left valve, Io.6190, × 140.

Procytherura aerodynamica sp. nov. (p. 204, see also Pl. 12, figs 1–3)
Middle or Upper Kimmeridgian, sample B219

FIG. 7. External view, right side, male carapace, holotype Io.6191, × 100.

FIG. 8. External view, left side, female carapace, paratype Io.6192, × 100.

FIG. 9. Internal view, juvenile right valve, paratype Io.6199, × 100.

FIGS 10, 16. External view, × 100 and enlargement of surface to show pitting, × 500, juvenile right valve, paratype Io.6200.

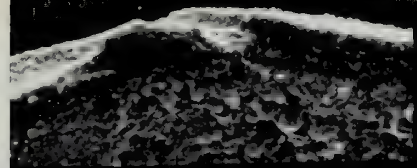
FIG. 11. External view, juvenile left valve, paratype Io.6203, × 100.

FIG. 12. External view, male right valve, paratype Io.6202, × 100.

FIG. 13. External view, female right valve, paratype Io.6193, × 100.

FIG. 14. Internal view, male left valve, paratype Io.6197, × 100.

FIG. 15. Internal view, female right valve, paratype Io.6196, × 100.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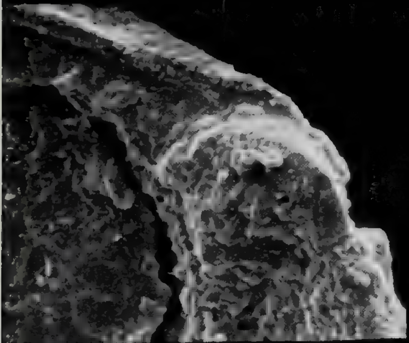
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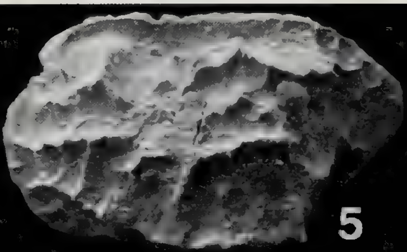
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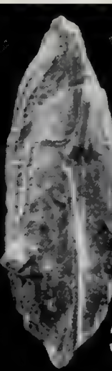
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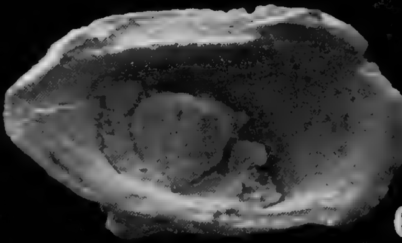
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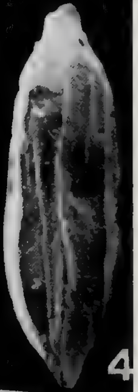
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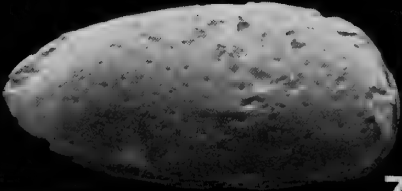
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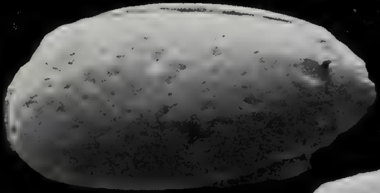
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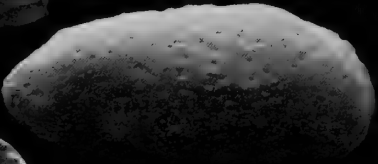
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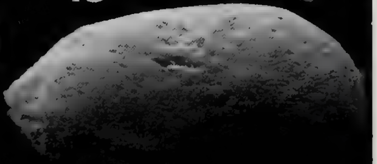
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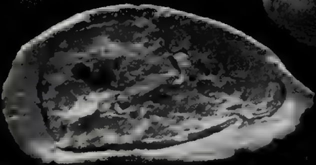
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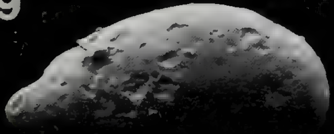
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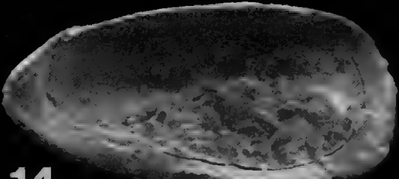
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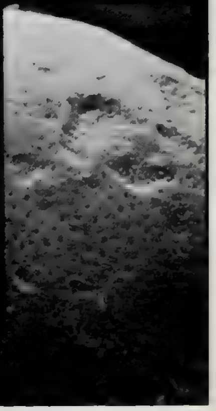
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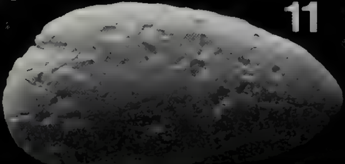
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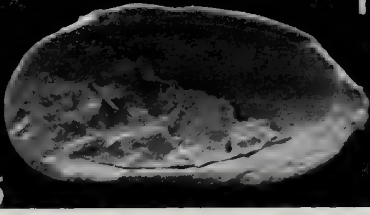
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PLATE 12

Procytherura aerodynamica sp. nov. (p. 204, see also Pl. 11, figs 7–16)
Middle or Upper Kimmeridgian, sample B219

FIG. 1. Enlargement of posterior hinge socket, female left valve, paratype Io.6198, × 500.

FIG. 2. Ventral view, male carapace, paratype Io.6194, × 100.

FIG. 3. Dorsal view, juvenile carapace, paratype Io.6195, × 100.

Procytherura sp. (p. 206)

FIG. 4. Middle Callovian, sample B97. Right side, complete carapace, Io.6209, × 150.

Cytheropteron (? Infracytheropteron) aitkeni sp. nov. (p. 206)
Lower and Middle or Upper Kimmeridgian

FIG. 5. External view, juvenile left valve, paratype Io.6217, sample B107a, × 140.

FIG. 6. External view, female right valve, paratype Io.6213, sample B219, × 140.

FIG. 7. External view, female left valve, holotype Io.6210, sample B219, × 140.

FIG. 8. Dorsal view, female carapace, paratype Io.6211, sample B219, × 140.

FIG. 9. External view, female left valve, paratype Io.6215, sample B104a, × 140.

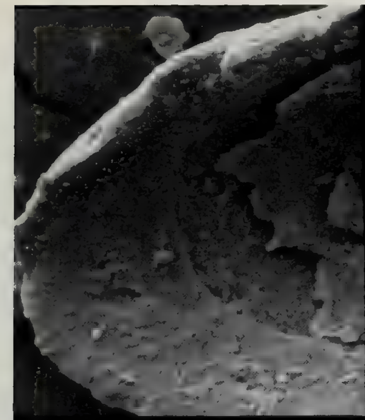
FIGS 10, 13. Internal view, female left valve, × 140, and muscle scars (anterior to right), × 1000, paratype Io.6214, sample B219.

FIG. 11. External view, male left valve, paratype Io.6212, sample B219, × 140.

FIG. 12. Dorsal view to show hinge bar and posterior terminal denticles, male right valve, paratype Io.6216, sample B223, × 140.

Cytheropteron grekoffi sp. nov. (p. 209, see also Pl. 13, figs 1–2)

FIG. 14. Upper Oxfordian, sample B67. External view, right side, complete carapace, paratype Io.6222, × 120.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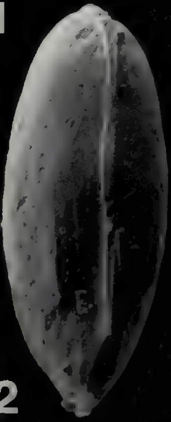
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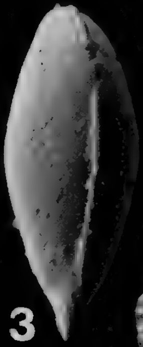
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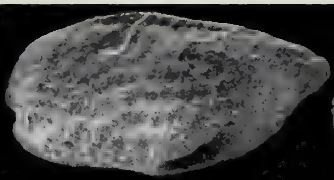
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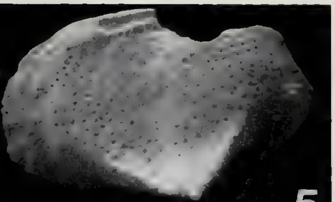
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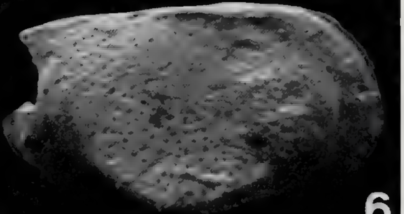
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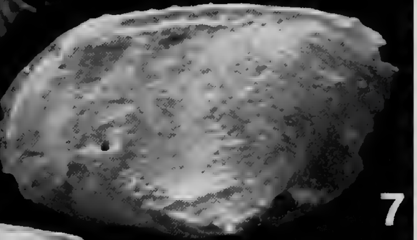
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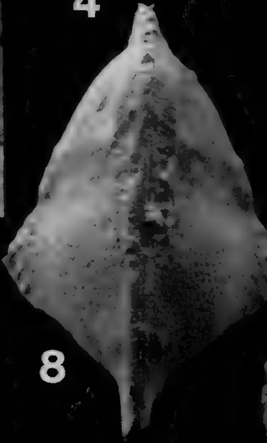
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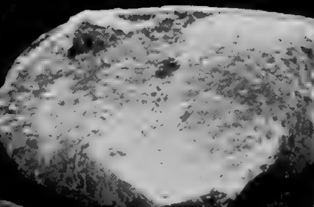
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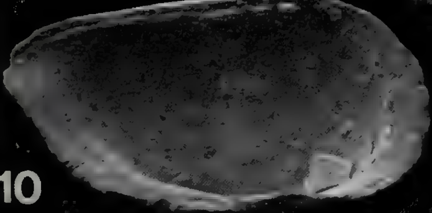
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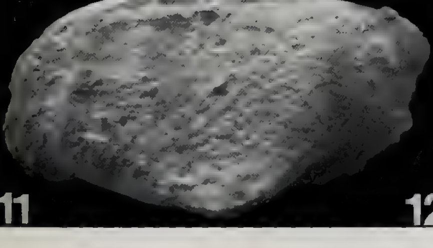
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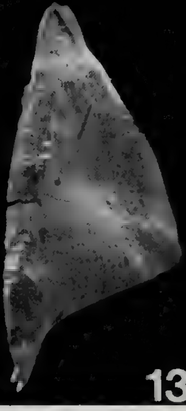
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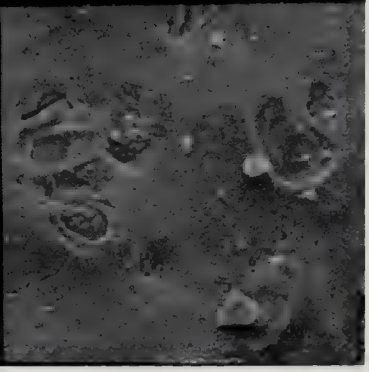
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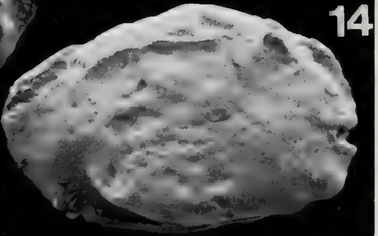
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PLATE 13

Cytheropteron grekoffi sp. nov. (p. 209, see also Pl. 12, fig. 14)
Upper Oxfordian

Fig. 1. External view, right side, complete carapace, holotype Io.6220, sample BM86, ×120.

Fig. 2. External view, left side, complete carapace, paratype Io.6221, sample B2, ×120.

Cytheropteron sp. (p. 210)
Middle or Upper Kimmeridgian, sample B223

Fig. 3. Ventral view, complete carapace, Io.6231, ×156.

Fig. 4. External view, right side, complete carapace, Io.6230, ×156.

Cytheropteron (Infracytheropteron) ndaui sp. nov. (p. 208)
Middle or Upper Kimmeridgian, sample B223

Fig. 5. External view, female carapace, holotype Io.6225, ×150.

Figs 6, 8. External and internal views, female left valve, paratype Io.6226, ×150.

Fig. 7. Internal view, female right valve, paratype Io.6228, ×150.

Fig. 9. Internal view, male left valve, paratype Io.6229, ×150.

Fig. 10. Dorsal view, male carapace, paratype Io.6227, ×150.

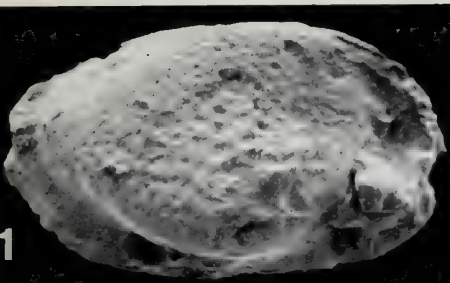
Acrocythere ? tricostata sp. nov. (p. 211)
Middle or Upper Kimmeridgian, sample B223

Fig. 11. External view, left valve, holotype Io.6241, ×150.

Fig. 12. Internal view, right valve, paratype Io.6244, ×150.

Fig. 13. Internal view, left valve, paratype Io.6242, ×150.

Fig. 14. External view, right valve, paratype Io.6243, ×150.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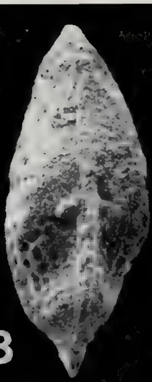
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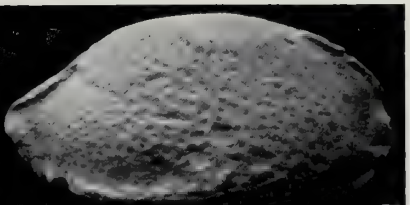
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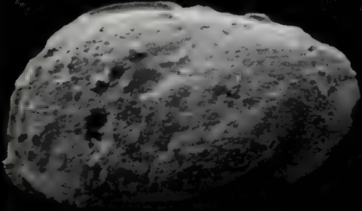
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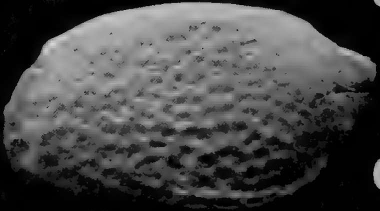
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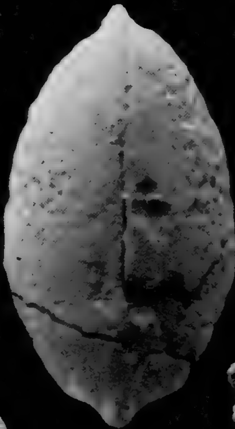
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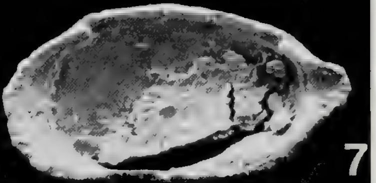
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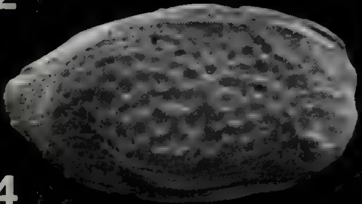
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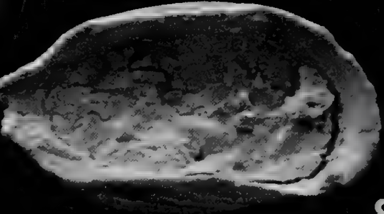
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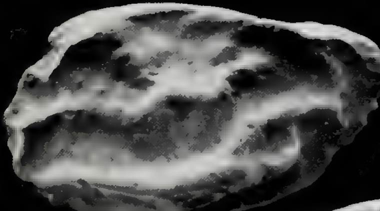
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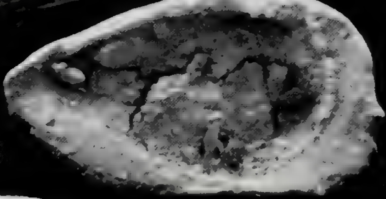
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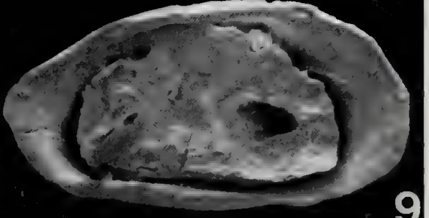
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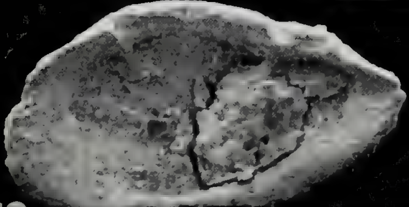
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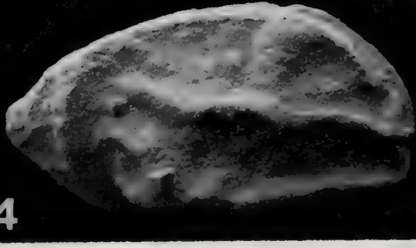
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PLATE 14

Paracytheridea mandawaensis sp. nov. (p. 210)
Middle or Upper Kimmeridgian, sample B223

Figs 1, 6. External view, left side, complete carapace, × 150, and muscle scars × 1000, holotype Io.6233.

Fig. 2. External view, right valve, paratype Io.6234, × 150.

Figs 3, 5. External view, left valve, × 150, and enlargement of ornamentation and of muscle scars, × 1000, paratype Io.6235.

Fig. 4. External view, right side, complete carapace, paratype Io.6239, × 150.

Fig. 7. Dorsal view, complete carapace, paratype Io.6236, × 150.

Fig. 8. Ventral view, complete carapace, paratype Io.6237, × 150.

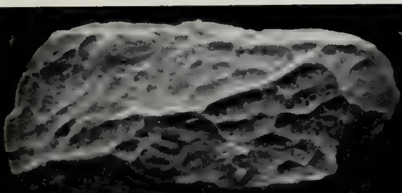
Fig. 9. Internal view, left valve, paratype Io.6238, × 150.

Looneyella africana sp. nov. (p. 212)
Middle or Upper Kimmeridgian, sample B223

Fig. 10. External view, female left valve, holotype Io.6246, × 150.

Fig. 11. External view, male right valve, paratype Io.6247, × 150.

Fig. 12. Internal view, male left valve, paratype Io.6248, × 150.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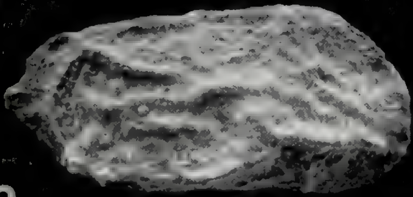
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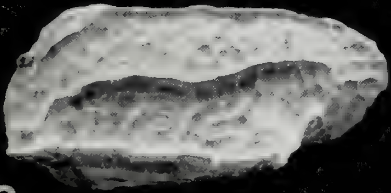
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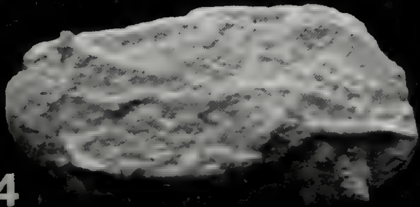
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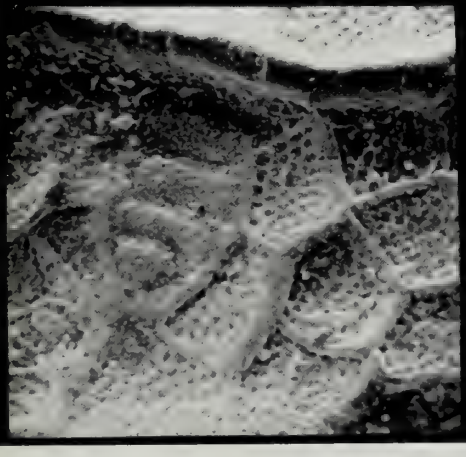
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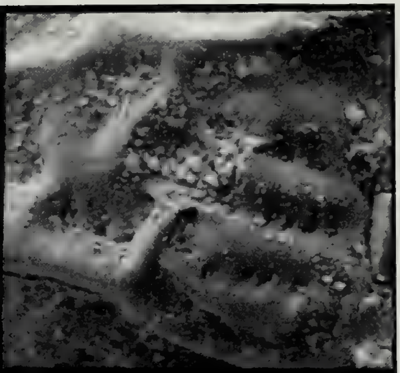
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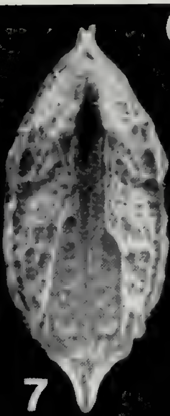
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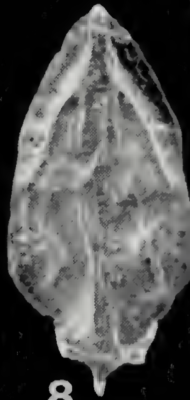
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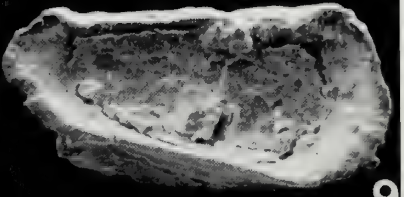
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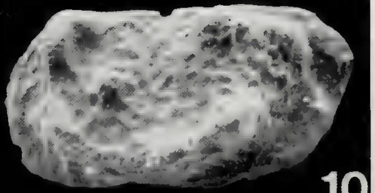
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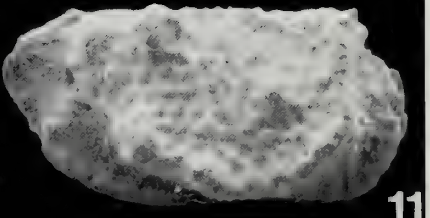
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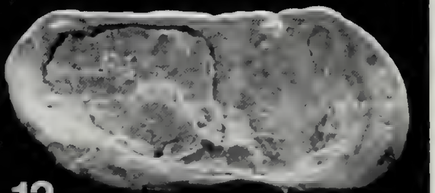
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G. L. EATON

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 26 No. 6
LONDON: 1976

DINOFLAGELLATE CYSTS FROM THE BRACKLESHAM BEDS (EOCENE) OF THE ISLE OF WIGHT, SOUTHERN ENGLAND

BY
GEOFFREY LEONARD EATON
BP Petroleum Development Ltd

Pp. 225–332 ; 21 *Plates* ; 31 *Text-figures*

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By G. L. EATON

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ABSTRACT

Dinoflagellate cysts considered to be indigenous to the Eocene are described from the Bracklesham Beds (Lower, Middle and Upper Eocene) of the Isle of Wight, southern England. A total of 106 taxa are recorded, including three new genera : *Achilleodinium*, *Araneosphaera* and *Distatodinium*, and 23 new species : *Araneosphaera araneosa*, *Areoligera sentosa*, *A. tauloma*, *A. undulata*, *Cyclonephelium spinetum*, *C. vicinum*, *Distatodinium craterum*, *Heteraulacacysta* ? *leptalea*, *Homotryblium abbreviatum*, *H. oceanicum*, *Hystrichokolpoma granulata*, *H. salacia*, *Hystrichosphaeridium asterium*, *Impletosphaeridium cracens*, *I. insolitum*, *I. luxurium*, *Kisselevia insolens*, *Lanternosphaeridium vectense*, *Phthanoperidinium alectrolophum*, *P. echinatum*, *P. tritonium*, *Turbiosphaera galatea* and *T. magnifica*. Five informal microplankton zones are defined for the Bracklesham Beds, based on the stratigraphical ranges of 70 dinoflagellate cyst species. The Bracklesham Beds at Whitecliff Bay and Alum Bay, Isle of Wight, are correlated using the microplankton zones. The recorded microplankton assemblages are compared with those described from the Lower Eocene of the London Basin and the Eocene of northern Europe. The most significant palynostratigraphical features of the recorded assemblages are listed and discussed in relation to microplankton assemblages from Palaeogene sediments throughout the world.

I. INTRODUCTION

The investigation of organic-walled microplankton (dinoflagellate cysts and acritarchs) from Palaeogene sediments in southern England has been conducted at Sheffield University under the supervision of Dr Charles Downie. Following the thesis work of Williams (1963) on the Lower Eocene London Clay of the Hampshire and London Basins, and Husain (1967) on the Palaeocene and Lower Eocene of the

London Basin, the present author has studied the Bagshot and Bracklesham Beds of the Isle of Wight in the Hampshire Basin where these sediments succeed the London Clay and include representatives of the Lower, Middle and Upper Eocene.

This study had two main objectives, to record and describe the organic-walled microplankton in these sediments, and to evaluate their potential for stratigraphical correlation.

The Bagshot Sands proved to be palynologically barren, but the Bracklesham Beds yielded rich assemblages of organic-walled microplankton, pollen and spores. The microplankton include dinoflagellate cysts which are considered to be indigenous to the Bracklesham Beds, reworked dinoflagellate cysts derived from Jurassic and Cretaceous sediments, acritarchs (including both indigenous and reworked forms), and members of the Chlorophyceae and Prasinophyceae. In this paper only the indigenous dinoflagellate cysts are described.

All type and figured specimens with a British Museum (Natural History) slide number quoted in this paper are lodged in the palaeontological collection of the British Museum (Natural History), London. Several of these specimens were figured in Eaton (1971a) where they were described as being housed in the Micropalaeontology Laboratory, Department of Geology, The University, Sheffield, Yorkshire, England. The original slide numbers in Eaton (1971a) and the corresponding British Museum (Natural History) slide numbers in this paper are :

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W51.1.	V.57759	AB28.1.	V.57788
W51.C1.	V.57760	AB40.1.	V.57790
W54.C1.	V.57761	AB40.2.	V.57791
W56.1.	V.57763	AB40.C1.	V.57794
W56.2.	V.57764	AB40.C2.	V.57795
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II. STRATIGRAPHY

Palaeogene sediments in southern England are essentially restricted to the Hampshire and London Basins (Fig. 1). These two areas are now structurally separated, but there is no evidence this was so during the Palaeogene, when they were both situated in the Anglo–Paris–Belgian depositional basin.

Eocene sediments outcrop in a narrow strip running east to west across the Isle of Wight from Whitecliff Bay to Alum Bay (Fig. 2). At these two localities the five main lithostratigraphical units of the Eocene are exposed in cliff sections : the basal Reading Beds resting on the eroded upper surface of the Chalk are succeeded by the London Clay, the Bagshot Sands, the Bracklesham Beds and the Barton Beds. At both localities the Bracklesham Beds are perfectly exposed in a vertical or near vertical attitude, and display a considerable variety of marine and non-marine sediments : sands, clays and sandy clays frequently yielding marine mollusca and foraminifera ; laminated beds consisting of alternating layers of sand and clay, with carbonaceous matter occurring in thin seams or scattered on the bedding

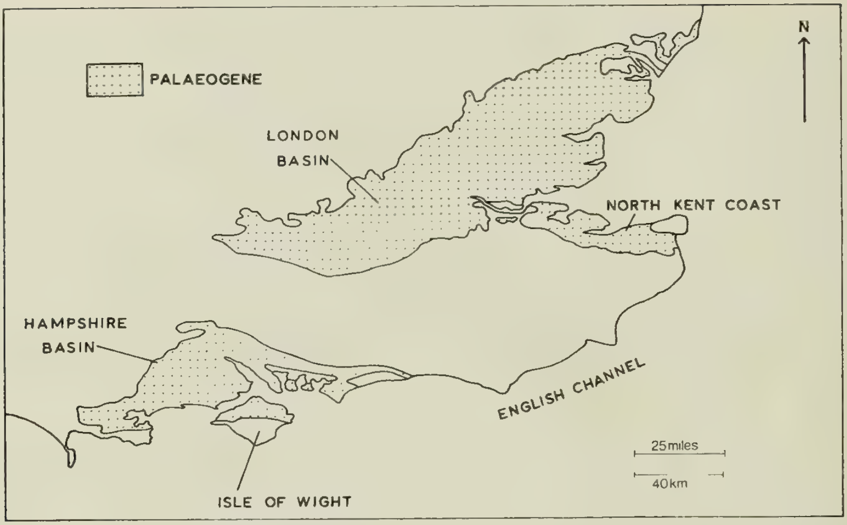
PALAEOGENE
LONDON BASIN
NORTH KENT COAST
HAMPSHIRE BASIN
ENGLISH CHANNEL
ISLE OF WIGHT
N
25 miles
40 km

FIG. 1. Map showing the major outcrops of Palaeogene sediments in southern England.

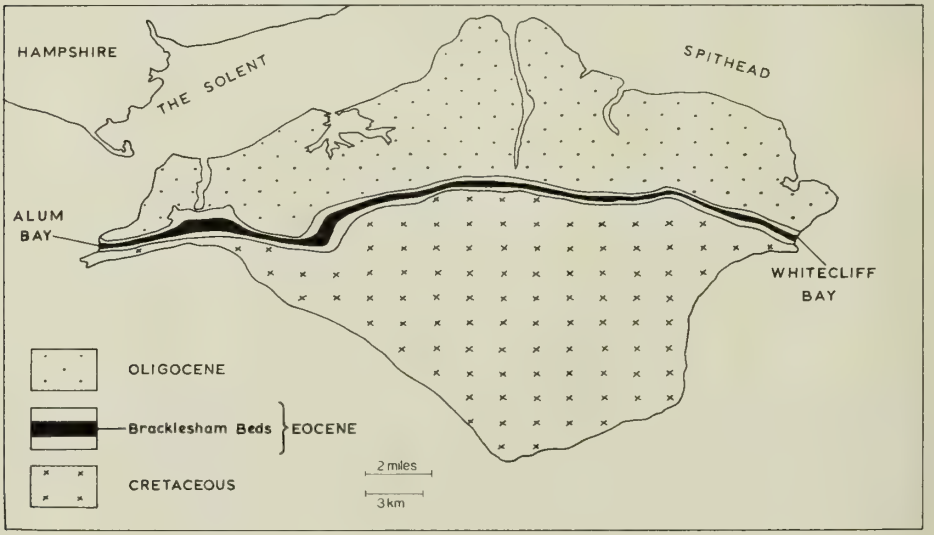
HAMPSHIRE
THE SOLENT
SPITHEAD
ALUM BAY
WHITECLIFF BAY
OLIGOCENE
Bracklesham Beds
EOCENE
CRETACEOUS
2 miles
3 km

FIG. 2. Generalized geological map of the Isle of Wight.

planes; brightly coloured barren sands which are typically cross-bedded; pebble beds, non-marine clays, pipeclays and lignite beds.

At Whitecliff Bay the type section of the Bracklesham Beds (Fisher 1862) is 182 m (598 ft) thick and consists mainly of sands, clays and sandy clays yielding a marine fauna, and laminated beds (Fig. 3). The minor differences between Fisher's interpretation of the lithological divisions within the Bracklesham Beds and that of the author are mainly due to variations in the degree of exposure in the section.

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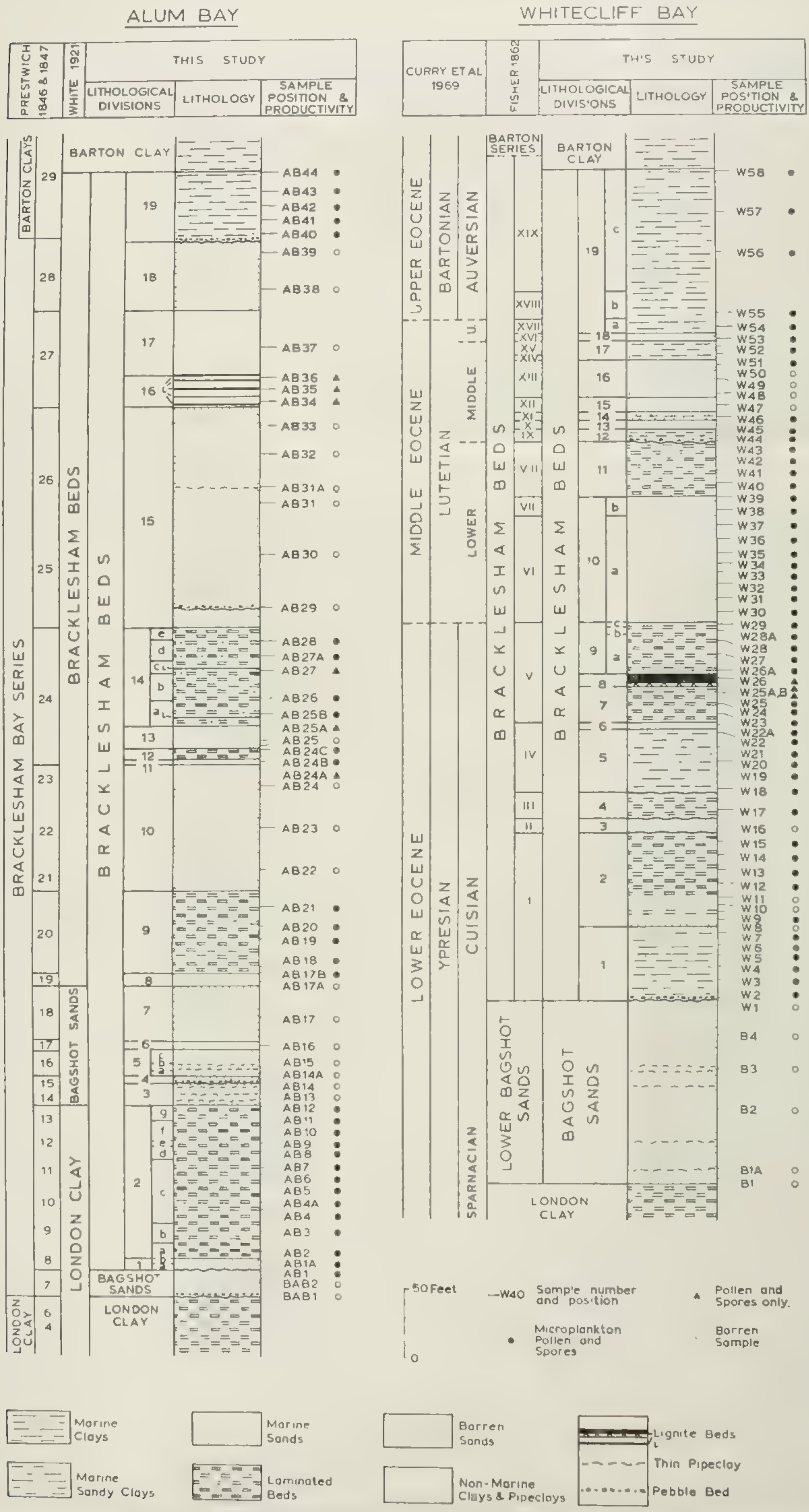
Fig. 5. The sections of the Bagshot Sands and the Bracklesham Beds exposed at Whitecliff Bay and Alum Bay, Isle of Wight, with sample positions and sample productivity.


ALUM BAY
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SAMPLE POSITION & PRODUCTIVITY
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BARTON CLAY
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WHITECLIFF BAY
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W44
W43
W42
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W32
W31
W30
W29
W28A
W28
W27
W26A
W26
W25A,B
W25
W24
W23
W22A
W22
W21
W20
W19
W18
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W16
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W10
W9
W8
W7
W6
W5
W4
W3
W2
W1
B4
B3
B2
B1A
B1
50 Feet
0
—W40 Sample number and position
▲ Pollen and Spores only.
● Microplankton Pollen and Spores
○ Barren Sample
Marine Clays
Marine Sandy Clays
Marine Sands
Laminated Beds
Barren Sands
Non-Marine Clays & Pipeclays
Lignite Beds
L
Thin Pipeclay
Pebble Bed

Fig. 3. The [illegible] Bagshot Sand and the Bracklesham Beds [illegible] at Whitecliff Bay and Alum Bay, I.O.W. [illegible] sample position and [illegible] productivity.

At Alum Bay the Bracklesham Beds are here considered to be 242 m (793 ft) thick and consist mainly of barren sands and laminated beds (Fig. 3). The positions of the top of the London Clay and the base of the Bracklesham Beds used in this study differ from the previously accepted interpretation (White 1921) in that the upper part of the London Clay of White is here assigned to the Bracklesham Beds, and the Bagshot Sands are represented by 6·1 m (20 ft) of grey and yellow sands. Apart from the inclusion of the Bagshot Sands this revised interpretation is comparable to Prestwich's concept of the London Clay and the Bracklesham Bay Series (Prestwich 1847). All interpretations of the latter part of the Alum Bay sequence are essentially based on lithological comparison with other sections. My lithological divisions within the Bracklesham Beds at Alum Bay have yet to be formally described, but they can be interpreted in terms of Prestwich's original subdivision of the sequence (Prestwich 1846).

The age of the Bracklesham Beds has been determined by comparing the marine faunas of mollusca and foraminifera in the Whitecliff Bay section with faunas from the Eocene of France and Belgium. The application of the French and Belgian stages to the Bracklesham Beds is discussed by Curry, Gulink & Pomerol (1969), and their interpretation is used here. The recognition of the Cuisian is based on the record of *Nummulites planulatus* in bed 5 (Fisher bed IV) by Wrigley & Davis (1937). Although there is no palaeontological evidence, they also assigned the Bagshot Sands and beds 1–4 (Fisher beds I–III) of the Bracklesham Beds to the Cuisian, but left the upper limit as indefinite. Between the horizon yielding *N. planulatus* and the greensands yielding *N. laevigatus*, there is an interval devoid of marine faunas (beds 7–9, Fisher bed V). Curry *et al.* consider this to represent the youngest part of the Cuisian. The recognition of the Lutetian is based on the presence of *N. laevigatus* in beds 10 and 11 (Fisher beds VI–VIII) and *N. variolarius* in beds 11–19a (Fisher beds VIII–XVII). The assignment of the highest Bracklesham Beds (bed 19b–c, Fisher beds XVIII and XIX) to the Auversian is based on faunal evidence from equivalent sediments at Huntingbridge, Hampshire.

The upper limit of the Bracklesham Beds is taken immediately below a horizon rich in *N. prestwichianus* which marks the base of the Barton Beds.

The Bracklesham Beds and the Bagshot Sands at Whitecliff Bay and Alum Bay were sampled for palynological study. All samples were prepared using the standard acid digestion technique. The sampled horizons and their palynological productivity are indicated in Fig. 3.

III. SYSTEMATIC DESCRIPTIONS

The 106 dinoflagellate cyst taxa recorded in this study and described in this section are assigned to three informal groups: the Gonyaulacacean and Peridiniacean Groups as described by Wall & Dale (1968a), and the Unknown Affinities Group for taxa not assignable to the two main groups. This procedure follows that adopted by Davey & Verdier (1971). The genera in each group are described in alphabetical order. In the systematic descriptions under 'DIMENSIONS', n indicates the number of specimens measured. The paragraph headed 'OCCURRENCE' includes the stratigraphical distribution of the species in the Bracklesham Beds of the Isle of Wight, quoted in terms of Lower, Middle and Upper Eocene. In the paragraph headed 'PREVIOUS RECORDS' an asterisk (e.g. De Coninck 1972*) indicates a listed record of the species without description or illustration.

Division *PYRRHOPHYTA*

Class *DINOPHYCEAE*

Order PERIDINIALES

GONYAULACACEAN GROUP

Genus ***ACHILLEODINIUM*** nov.

DERIVATION OF NAME. From Achilles, Greek hero of the Trojan War.

DIAGNOSIS. Dinoflagellate cysts having a spherical or subspherical body bearing two types of intratabular processes: cylindrical processes, one per reflected plate area, hollow, circular to polygonal in cross-section, distally open or closed, variable in size; the larger processes occurring on the pre- and postcingular and antapical zones, the smaller on the apical zone. Slender processes, simple or bifurcate, distally open, restricted to the cingular and sulcal zones. Reflected tabulation 4′, 6″, 6c, 5‴, 1p, 1⁗; archaeopyle precingular, formed by displacement of plate 3″.

TYPE SPECIES. *Hystrichosphaeridium biformoides* Eisenack 1954; Upper Eocene, East Prussia.

REMARKS. *Achilleodinium* n. gen. is similar to *Hystrichokolpoma* Klumpp 1953 emend. Williams & Downie 1966a and *Florentinia* Davey & Verdier 1973 in both overall morphology and reflected tabulation. *Hystrichokolpoma* is distinguished by having an apical tetratabular archaeopyle. In *Florentinia* the archaeopyle is formed by displacement of precingular plate 3″ with breakage or displacement of the apical plates. In *Achilleodinium* the archaeopyle is formed exclusively by displacement of plate 3″, and there is no breakage or displacement of the apical plates.

Achilleodinium biformoides (Eisenack 1954) n. comb., emend. herein

Fig. 4; Pl. 1, figs 1–6

1954 *Hystrichosphaeridium biformoides* Eisenack: 68; pl. 11, figs 16–20.
1963 *Baltisphaeridium biformoides* (Eisenack) Downie & Sarjeant: 91.
1965 *Hystrichokolpoma biformoides* (Eisenack) Eisenack: 151; pl. 14, fig. 2.
1965 *Hystrichokolpoma biformoides* (Eisenack) Rozen: 22; pl. 3, figs 1–2; text-fig. 19.
1966a *Hystrichokolpoma biformoides* (Eisenack) Morgenroth: 28; pl. 6, figs 9–10.
1967 *Hystrichokolpoma* sp. [? *H. biformoides* (Eisenack)] Cookson & Cranwell: 206; pl. 1, fig. 11.
1967 *Hystrichokolpoma biformoides* (Eisenack) Morgenroth; Agelopoulos: 40; pl. 13 figs 5–6.
1972 *Hystrichokolpoma cinctum* Klumpp; Benedek: 28; pl. 9, fig. 7; not pl. 8, fig. 8.

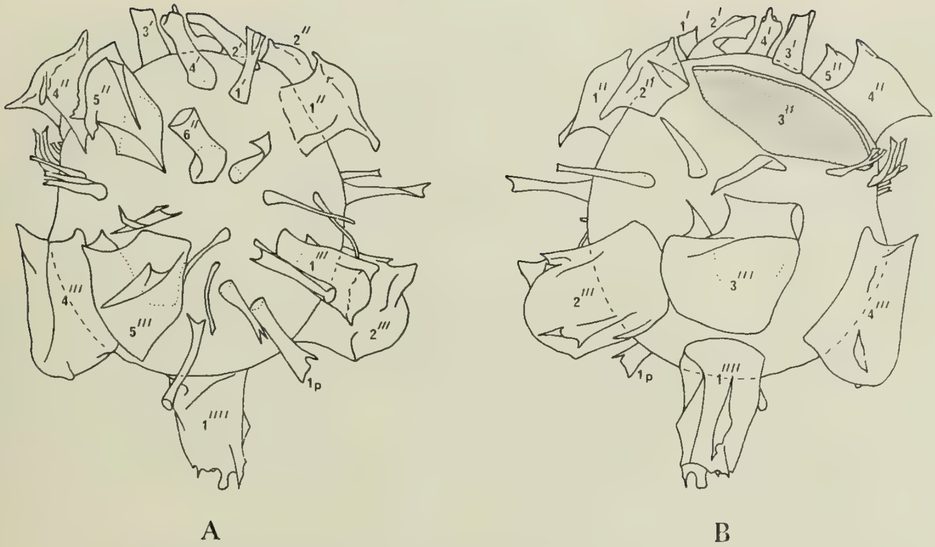

FIG. 4. *Achilleodinium biformoides* (Eisenack 1954) n. comb., emend., reflected tabulation. A. Ventral view. B. Dorsal view. The precingular archaeopyle (3″) is indicated by shading. V.57759 (12); W51.

EMENDED DIAGNOSIS. Cyst body spherical or subspherical with a smooth or finely granular surface. Processes intratabular, variable in size and shape, with a striated or finely fibrous appearance. Apical processes relatively narrow, typically open distally. Precingular processes 1″–5″, and postcingular processes 2‴–5‴, are large, broad, circular to polygonal in cross-section, and usually distally expanded and closed. Processes 6″ and 1‴ are relatively reduced. Cingular processes are slender, hollow, distally open, usually two, but sometimes one per reflected plate area. Sulcal processes similar to those on the cingular and apical zones. Antapical process usually longer than the other large processes. Reflected tabulation 4′, 6″, 6c, 5‴, 1p, 1⁗; archaeopyle precingular, formed by displacement of plate 3″.

HOLOTYPE. The specimen figured as *Hystrichosphaeridium biformoides* by Eisenack (1954: pl. 11, fig. 18), Upper Eocene, East Prussia.

DIMENSIONS. Holotype: overall diameter 70 μ; diameter of cyst body 50 μ. Observed range: diameter of cyst body 42–63 μ; large processes, length up to 22 μ, breadth up to 28 μ; length of slender processes up to 17 μ. (n = 14).

REMARKS. The large processes frequently exhibit longitudinal folds, spines or tubules on the distal margin, and broad fenestrations at the proximal margin of the process wall. The distal margin in the open processes may be expanded, is irregular and often deeply incised. In some processes the incision extends to the proximal margin (Fig. 4A). Reduced precingular process 6″ is similar to the apical processes. Reduced postcingular process 1‴ is similar to the precingular processes. The other postcingular processes are usually larger than the precingular processes. Although the antapical process is usually the longest, it may be relatively narrow ; its spines or tubules may be developed towards, but not actually at the distal margin. The specimen of *A. biformoides* figured by Morgenroth (1966a : pl. 6, figs 9–10) has an antapical process considerably longer (40 μ) than in specimens observed in this study. The overall range of form of the processes readily distinguishes *A. biformoides* from described species of *Hystrichokolpoma*, when its precingular archaeopyle is not exhibited.

Occurrence. Lower, Middle and Upper Eocene.

Previous Records. Lower Eocene of Belgium (Morgenroth 1966a ; (?) De Coninck 1972*, questionably as *Hystrichokolpoma* ? *biformoides*) and of north Germany (Morgenroth 1966a) ; Middle Eocene of northern France (Gruas-Cavagnetto 1971*) ; Upper Eocene of Belgium (Rozen 1965), of East Prussia (Eisenack 1954, 1965) and of north Germany (Agelopoulos 1967) ; Eocene, undifferentiated, of Chile (Cookson & Cranwell 1967, questionably as *Hystrichokolpoma* sp.) ; Middle and Upper Oligocene of north Germany (Benedek 1972, pl. 9, fig. 7 only).

Genus ***ACHOMOSPHAERA*** Evitt 1963

Achomosphaera ramulifera (Deflandre) Evitt 1963

Pl. 1, fig. 7

1937 *Hystrichosphaeridium ramuliferum* Deflandre : 74 ; pl. 14, figs 5–6 ; pl. 17, fig. 10.
1963 *Achomosphaera ramulifera* (Deflandre) Evitt : 163, text-fig. 2.

Dimensions. Observed range : diameter of cyst body 31–50 μ ; length of processes up to 22 μ. (n = 17).

Occurrence. Lower, Middle and Upper Eocene.

Previous Records. Lower Cretaceous, Albian (Davey & Verdier 1971), to Pliocene (Habib 1971) ; probably world-wide in distribution.

Achomosphaera alcicornu (Eisenack) Davey & Williams 1966a

Pl. 1, fig. 11

1954 *Hystrichosphaeridium alcicornu* Eisenack : 65 ; pl. 10, figs 1–2 ; text-fig. 5.
1966a *Achomosphaera alcicornu* (Eisenack) Davey & Williams : 50 ; pl. 5, fig. 3.

Dimensions. Observed range : cyst body 52 × 42 μ to 70 × 62 μ ; length of processes up to 30 μ. (n = 16).

Remarks. This species is morphologically similar to *Spiniferites pseudofurcatus* (Klumpp) Sarjeant 1970, and is distinguished by the absence of plate boundaries on the cyst body.

Occurrence. Lower, Middle and Upper Eocene.

Previous Records. Palaeocene of north Germany (Gocht 1969) and of northern Spain (Caro 1973) ; Lower Eocene of Belgium (De Coninck 1965, 1967*, 1968), of northern France (Gruas-Cavagnetto 1968, 1970b*), of north Germany (Gocht 1969), of northern Spain (Caro 1973) and of the Hampshire and London Basins in southern England (Davey & Williams 1966a ; Downie, Husain & Williams 1971) ; Middle Eocene of north Germany (Agelopoulos 1967, Gocht 1969) ; Upper Eocene of Belgium (Rozen 1965), of East Prussia (Eisenack 1954) and of north Germany (Agelopoulos 1967) ; ? Upper Eocene of north Germany (Gocht 1969) ; Eocene, undifferentiated, of the eastern seaboard, U.S.A. (subsurface, offshore, Habib 1972) and of Romania (Balteş 1969, as *Perisseiasphaeridium pannosum*) ; Middle Oligocene of north Germany (Gerlach 1961, Gocht 1969, Benedek 1972) ; Upper Oligocene of north Germany (Benedek 1972) ; ? Middle Miocene of north Germany (Gerlach 1961).

Achomosphaera membraniphora (Agelopoulos 1964) n. comb., emend. herein

Fig. 5 ; Pl. 1, figs 8–10

1964 *Hystrichostrogylon membraniphorum* Agelopoulos : 674 ; figs 1–2.

Emended Diagnosis. A smooth unornamented species of *Achomosphaera* in which the periphragm is separated from the endophragm at the antapex and over the ventral surface, forming a distinct pericoel in this region. The processes developed over the area of the pericoel are shorter than the other processes present on the cyst body.

Dimensions. Observed range: diameter of cyst body 28–48 μ ; height of pericoel 6–20 μ ; length of processes up to 24 μ. ($n = 18$).

Remarks. In process form and distribution, and archaeopyle position, *A. membraniphora* is directly comparable to the typical Palaeogene form of *Achomosphaera ramulifera*, and is only distinguished by the development of the pericoel. Agelopoulos (1964, 1967) described this form as the type species of *Hystrichostrogylon*, and he considered the archaeopyle to be apical in position. His illustrations show lateral views of several specimens, and in this orientation a precingular archaeopyle can appear to be apical – compare with the illustrated specimen of *Spiniferites* sp. (as *Hystrichosphaera* sp.) in Evitt (1967 : pl. 4, fig. 14). The precingular position of the archaeopyle is further confirmed by specimens, e.g. Fig. 5 and Pl. 1, fig. 8, examined here, and for this reason *Hystrichostrogylon membraniphorum* is here transferred to *Achomosphaera* Evitt 1963. Davey & Verdier (1971 : 34) maintained that *Spiniferites paradoxus* (Cookson & Eisenack) Sarjeant 1970 and *H. membraniphorum* 'were proposed to accommodate identical specimens', and that pericoel development in this group of dinoflagellate cysts does not warrant special taxonomic treatment. Specimens originally assigned to *H. membraniphorum* show no indication of sutural ridges reflecting a tabulation, and therefore they are referable to *Achomosphaera* rather than *Spiniferites*. Pericoel development in *Spiniferites* is

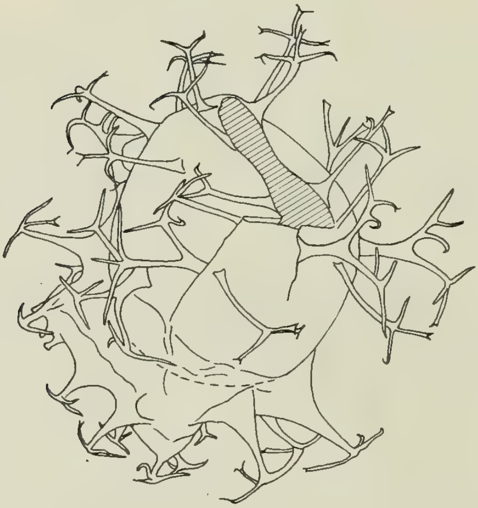

FIG. 5. *Achomosphaera membraniphora* (Agelopoulos 1964) n. comb., emend. Specimen showing the precingular archaeopyle (3″) indicated by shading, and the ventral pericoel. The broken line indicates the margin of the endophragm within the pericoel. V.57797 (3); AB40.

only known in specimens of Cretaceous age, while forms assignable to *A. membraniphora* have not been recorded from pre-Eocene sediments; the latter does seem to warrant special taxonomic treatment.

OCCURRENCE. Middle and Upper Eocene.

PREVIOUS RECORDS. Upper Eocene of north Germany (Agelopoulos 1964, 1967).

Genus ***ADNATOSPHAERIDIUM*** Williams & Downie 1966c

Adnatosphaeridium vittatum Williams & Downie 1966c

Pl. 2, fig. 1

1966c *Adnatosphaeridium vittatum* Williams & Downie: 215; pl. 24, figs 3, 7; text-fig. 56.

DIMENSIONS. Observed range: cyst body (without operculum) 35 × 36 μ to 44 × 48 μ; processes, length up to 30 μ, breadth up to 20 μ. (n = 10).

REMARKS. The processes show considerable variation in breadth and are frequently very broad (up to 20 μ). Distally they are united by interconnecting ribbon-like trabeculae which are particularly broad and membranous in the vicinity of the interconnections.

OCCURRENCE. Lower, Middle and Upper Eocene.

PREVIOUS RECORDS. Palaeocene of northern Spain (Caro 1973, doubtful attribution); Lower Eocene of the London Basin in southern England (Williams & Downie 1966c).

Adnatosphaeridium multispinosum Williams & Downie 1966c

Pl. 2, fig. 2

1966c *Adnatosphaeridium multispinosum* Williams & Downie : 216 ; pl. 24, fig. 5 ; text-fig. 58.

Description. Specimens here assigned to *A. multispinosum* have numerous typically slender processes, which are simple or branched and distally united by slender trabeculae bearing numerous erect spines. The processes rarely exceed half the mean diameter of the cyst body in length, and may appear to be irregularly distributed on it, or may be organized into arcuate, soleate or annular complexes.

Dimensions. Observed range : cyst body $30 \times 36\ \mu$ to $46 \times 58\ \mu$; length of processes up to $28\ \mu$. (n = 22).

Remarks. In addition to the typical forms of *A. multispinosum*, specimens have been recorded which show a reduction in the number of trabeculae, resulting in some of the processes being distally free.

Occurrence. Lower, Middle and Upper Eocene.

Previous Records. Palaeocene of northern Spain (Caro 1973) ; Lower Eocene of northern Spain (Caro 1973) and of the Hampshire Basin in southern England (Williams & Downie 1966c) ; Middle Eocene of northern France (Gruas-Cavagnetto 1971*).

Adnatosphaeridium robustum (Morgenroth 1966a) n. comb.

Pl. 2, fig. 3

1966a *Cannosphaeropsis robustum* Morgenroth : 19, pl. 4, fig. 1.

Description. Cyst body subspherical to ellipsoidal with a finely granular surface. Processes slender, typically simple, rarely branched, distally expanded and united by trabeculae of variable breadth. Acuminate spines occasionally present on the trabeculae. Archaeopyle apical, tetratabular.

Dimensions. Observed range : diameter of cyst body $37-50\ \mu$; length of processes up to $26\ \mu$. (n = 6).

Remarks. Specimens recorded here exhibit an apical, tetratabular archaeopyle, and are thus attributable to *Adnatosphaeridium*. *A. robustum* is distinguished from *A. vittatum* Williams & Downie 1966c by not having broad processes, and from *A. multispinosum* Williams & Downie 1966c by having fewer processes, and only occasionally showing the development of spines on the trabeculae.

Occurrence. Lower Eocene.

Previous Records. Lower Eocene of northern France (Gruas-Cavagnetto 1970b) and of north Germany (Morgenroth 1966a).

Genus ***ARANEOSPHAERA*** nov.

Derivation of Name. Latin, *araneum*, cobweb, with reference to the form of the membrane which distally unites the processes in this genus.

DIAGNOSIS. Dinoflagellate cysts having a spherical or subspherical body with a smooth or finely fibro-reticulate surface. Processes intratabular, fibrous, simple or branched. A variable proportion of the processes are distally united by fibrous membrane. Processes invariably present on the apical, pre- and postcingular and antapical zones. Typically each reflected plate area has one process, sometimes more than one. Cingular zone usually, but not invariably, devoid of processes. Basic reflected tabulation 4′, 6″, 5–6‴, 0–1p, 1⁗; archaeopyle precingular, formed by displacement of plate 3″.

TYPE SPECIES. *Araneosphaera araneosa* gen. et sp. nov.; Bracklesham Beds, Upper Eocene, Isle of Wight, England.

REMARKS. In the form and fibrous nature of its processes, and the position of its archaeopyle, *Araneosphaera* n. gen. is similar to *Cordosphaeridium* Eisenack 1963b emend. Morgenroth 1968, but is distinguished from the latter by having a membrane distally uniting its processes, and usually by not having processes on the cingular zone. Eisenack (1963b) probably encountered specimens attributable to *Araneosphaera* which he included in *Cordosphaeridium*, since in his original diagnosis for the latter genus, describing the processes, he says: 'At the tips the fibres diverge in paintbrush-like fashion, however may also unite together in net-like fashion' (translated from German in Norris & Sarjeant 1965 : 20). Morgenroth (1968 : pl. 45, fig. 9) figured a specimen from the Danian, attributing it to *Cordosphaeridium inodes* (Klumpp) Eisenack 1963b emend. Morgenroth 1968, in which there is clearly membrane distally uniting the processes. Whether this should be assigned to *Araneosphaera* cannot be determined until the distribution of its processes is known. In *Araneosphaera* the distal membrane frequently shows fenestrations, but the individual areas of membrane can rarely be described as trabeculate. In having distally united processes, *Araneosphaera* shows some similarity to *Adnatosphaeridium* Williams & Downie 1966c and *Cannosphaeropsis* O. Wetzel 1933 emend. Williams & Downie 1966c. *Adnatosphaeridium* does not have fibrous processes, and the archaeopyle is apical, tetratabular. *Cannosphaeropsis* similarly does not have fibrous processes, and although the archaeopyle is precingular, this genus is distinguished by the sutural position of its processes. *Membranilarnacia* Eisenack 1963a emend. Williams & Downie 1966c has distally united processes which may be fibrous, but is distinguished from *Araneosphaera* by having an apical, tetratabular archaeopyle. In having a cingular zone which is usually, but not invariably, devoid of processes, and additional processes on the hypotract between the primary postcingular processes and the antapical process, *Araneosphaera* shows some similarity to *Areosphaeridium* Eaton 1971a. The latter is distinguished by its apical, tetratabular archaeopyle, the distinctive form of its processes, and the absence of membrane distally uniting the processes.

Araneosphaera araneosa n. sp.

Fig. 6; Pl. 2, figs 5–8

DERIVATION OF NAME. Latin, *araneosus*, full of webs, with reference to the appearance of this species.

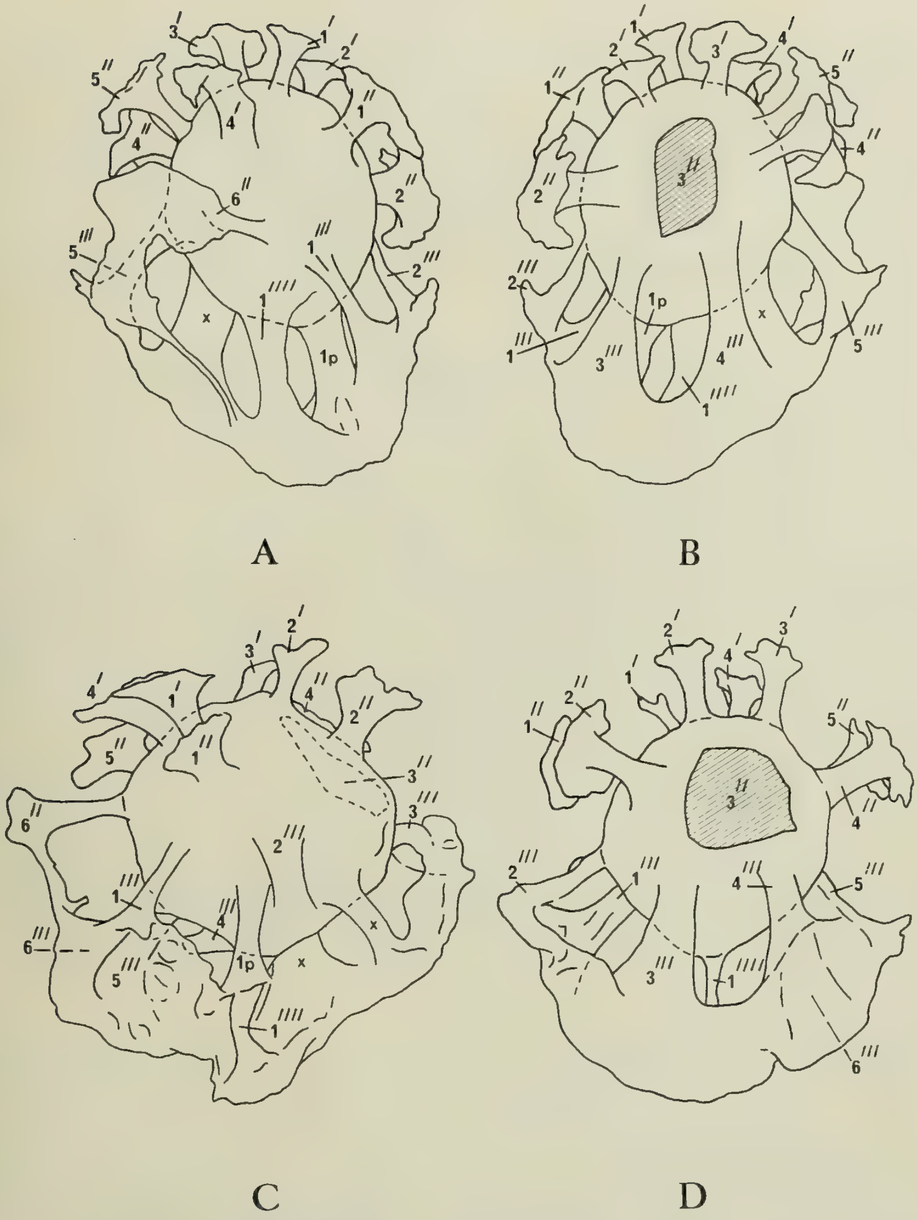
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FIG. 6. *Araneosphaera araneosa* gen. et sp. nov., reflected tabulation. A, B. Holotype, ventral and dorsal views respectively. The precingular archaeopyle (3'') is indicated by shading. V.57765 (2); W56. C. Ventral view; the broken line indicates the position of the archaeopyle on the dorsal surface. V.57793 (1); AB40. D. Dorsal view; the archaeopyle is indicated by shading. V.57797 (1); AB40. In A, B and C, x indicates additional processes.

Diagnosis. Cyst body spherical or subspherical with a smooth or finely fibro-reticulate surface. Processes intratabular, fibrous, simple or branched, proximally and distally expanded, may exhibit stem fenestration. Apical and precingular processes short, usually distally free, one per reflected plate area. Cingular zone typically devoid of processes, but an occasional one may be present. Processes on postcingular and antapical zones longer than those on the epitract, distally united by a usually irregularly fenestrate fibrous membrane. On these zones there is basically one process per reflected plate area. Additional processes are present, intermediate in position between the postcingular and antapical processes. Reflected tabulation 4′, 6″, 5–6‴, 0–1p, 1⁗; archaeopyle precingular, formed by displacement of plate 3″.

Holotype. B.M.(N.H.) Palaeont. slide V.57765 (2). Sample W56, bed 19c, Bracklesham Beds, Upper Eocene, Whitecliff Bay, Isle of Wight, England.

Dimensions. Holotype: overall $103 \times 82\ \mu$; diameter of cyst body $50\ \mu$; length of processes up to $38\ \mu$. Observed range: overall $94 \times 83\ \mu$ to $110 \times 110\ \mu$; diameter of cyst body $44–58\ \mu$; length of processes up to $43\ \mu$. $(n = 20)$.

Remarks. The majority of the apical and precingular processes are typically distally free. Occasionally some of these processes may be distally united, while process 6″ is usually distally united across the cingular zone with the postcingular processes. Occasionally a process can be interpreted as being cingular in position, but the cingular zone is typically devoid of processes. The precingular and antapical processes are always distally united by fibrous membrane which frequently shows the development of irregular fenestrations. These processes are often branched, and may show stem fenestration. Up to four additional processes have been observed between, and distally united with, the five or six primary postcingular processes and the antapical process. One of these is interpreted as reflecting the posterior intercalary plate (1p), while the others possibly represent additional process development on the postcingular zone. The combination of process form and distribution, archaeopyle position, and the presence of membrane distally uniting the hypotractal processes, distinguishes *Araneosphaera araneosa* n. sp. from all described species of dinoflagellate cyst.

Occurrence. Middle and Upper Eocene.

Genus ***AREOLIGERA*** Lejeune-Carpentier 1938 emend. Williams & Downie 1966c

The ***Areoligera senonensis*** complex

The genus *Areoligera* was defined by Lejeune-Carpentier (1938), *Areoligera senonensis* being the type species, with two other clearly related species, *A. coronata* and *A. medusettiformis*, distinguished essentially by the form of their processes. The description of all three species was based on specimens from the Upper Cretaceous (Senonian) of Belgium and Germany, and they are characterized by the development of process complexes on the dorsal surface of the cyst body. On the ventral surface the processes are restricted to the peripheral zone as in *Cyclonephelium* Deflandre & Cookson 1955 emend. Williams & Downie 1966c.

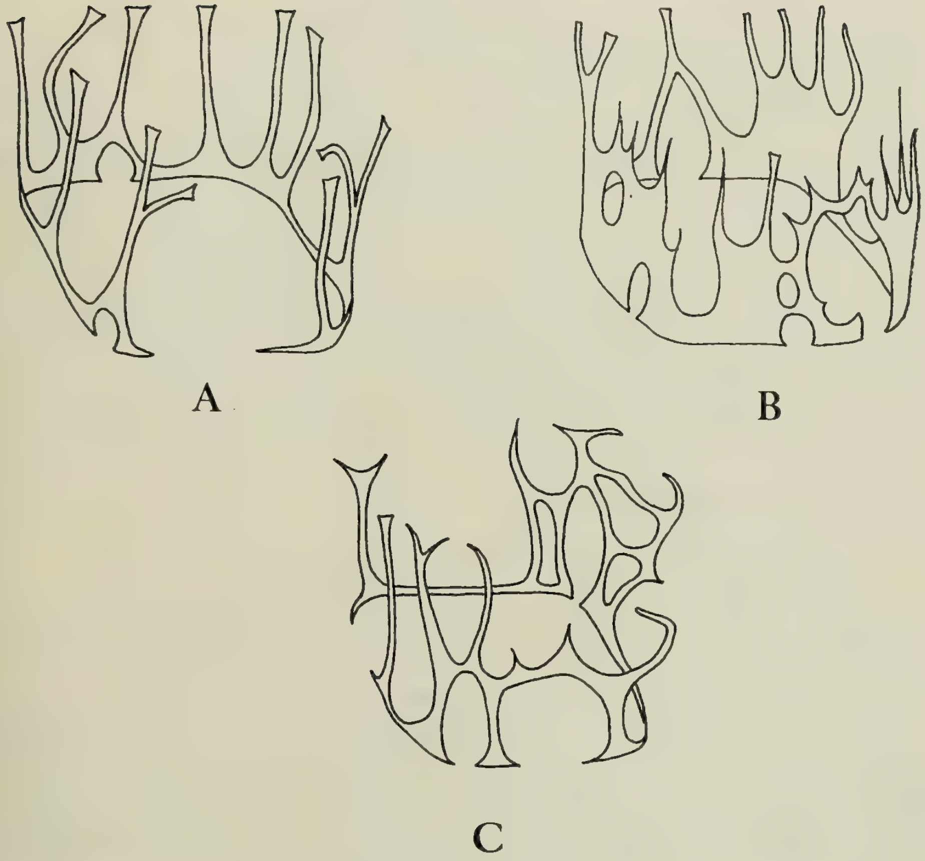


Fig. 7. Diagrammatic representation of process form in the *Areoligera senonensis* complex. A. *Areoligera senonensis* Lejeune-Carpentier 1938 and *A.* cf. *senonensis.* B. *Areoligera coronata* (O. Wetzel) Lejeune-Carpentier 1938 and *A.* cf. *coronata.* C. *Areoligera medusettiformis* (O. Wetzel) Lejeune-Carpentier 1938 and *A.* cf. *medusettiformis.*

Specimens assignable to *A. senonensis*, *A. coronata* and *A. medusettiformis* are here recorded in association with morphologically similar forms in which process complexes are developed on the ventral and dorsal surfaces. The latter forms were also recorded from the Lower Eocene of southern England by Williams & Downie 1966c as *A.* cf. *senonensis*, *A.* cf. *coronata* and *A.* cf. *medusettiformis*, with a reflected tabulation of 4′, 6″, 5‴, 1p, 1⁗.

These six closely related taxa are here considered to represent the morphological extremes of what is informally termed the *Areoligera senonensis* complex. Three basic process types are present in the forms assigned to this complex (Fig. 7). The majority of the specimens examined exhibit more than one process type, although, apart from transitional forms, one type is dominant. The six taxa have been distinguished on the basis of the following features :

Areoligera senonensis : The majority of the processes are simple, slender, frequently distally expanded, and usually proximally united by a low membrane (Fig. 7A). Process complexes are only developed on the dorsal surface.

Areoligera cf. *senonensis* : Dominant process form as in *A. senonensis* ; process complexes are developed on the ventral and dorsal surfaces.

Areoligera coronata : The majority of the processes are broad and membranous, frequently fenestrate, and have a digitate distal margin (Fig. 7B). Process complexes are only developed on the dorsal surface.

Areoligera cf. *coronata* : Dominant process form as in *A. coronata* ; process complexes are developed on the ventral and dorsal surfaces.

Areoligera medusettiformis : The majority of the processes are slender, distally expanded, and as well as being typically proximally united by a low membrane, adjacent processes are united by arched trabeculae which usually bear free spines (Fig. 7C). Process complexes are only developed on the dorsal surface.

Areoligera cf. *medusettiformis* : Dominant process form as in *A. medusettiformis* ; process complexes are developed on the ventral and dorsal surfaces.

Areoligera senonensis Lejeune-Carpentier 1938

Pl. 3, fig. 1

1938 *Areoligera senonensis* Lejeune-Carpentier : B164, text-figs 1–3.

Dimensions. Observed range : cyst body (without operculum) 36 × 48 μ to 42 × 60 μ ; length of processes up to 18 μ. (n = 2).

Occurrence. Lower Eocene.

Previous Records. Upper Cretaceous (Senonian) of Belgium (Lejeune-Carpentier 1938) ; Palaeocene and Lower Eocene of the London Basin in southern England (Downie, Husain & Williams 1971) ; Lower Eocene of northern France (Gruas-Cavagnetto 1970b) ; Middle Eocene of northern France (Gruas-Cavagnetto 1971*).

Areoligera cf. ***senonensis*** Lejeune-Carpentier 1938

Pl. 3, figs 4–5

1966c *Areoligera* cf. *senonensis* Lejeune-Carpentier ; Williams & Downie ; 230 ; pl. 25, fig. 6 ; text-fig. 64.

Dimensions. Observed range : cyst body (without operculum) 42 × 56 μ to 69 × 84 μ ; length of processes up to 20 μ. (n = 14).

Occurrence. Lower and Middle Eocene.

Previous Records. Palaeocene and Lower Eocene of north Germany (Gocht 1969, as *Areoligera senonensis*) and of the London Basin in southern England (Williams & Downie 1966c, Downie, Husain & Williams 1971*) ; Middle Eocene and questionably from the Middle Oligocene of north Germany (Gocht 1969, as *Areoligera senonensis*).

Areoligera coronata (O. Wetzel) Lejeune-Carpentier 1938

Pl. 3, fig. 2

1933 *Hystrichosphaera penicillata* (Ehrenberg) O. Wetzel forma *coronata* O. Wetzel : 41 ; pl. 4, fig. 17.
1938 *Areoligera coronata* (O. Wetzel) Lejeune-Carpentier : B170, text-fig. 6.

DIMENSIONS. Observed range : cyst body (without operculum) 40 × 54 μ to 58 × 66 μ ; length of processes up to 18 μ. (n = 5).

OCCURRENCE. Lower Eocene.

PREVIOUS RECORDS. Upper Cretaceous (Senonian) of north Germany (O. Wetzel 1933) ; Upper Cretaceous (Maastrichtian) of New Jersey, U.S.A. (Evitt 1961, as *Areoligera* cf. *senonensis*), and of Denmark (Wilson 1971, as *A. senonensis* – pl. 3, fig. 9 only) ; Lower Eocene of northern Spain (Caro 1973), and of the Hampshire and London Basins in southern England (Williams & Downie 1966c) ; Middle Eocene of northern France (Gruas-Cavagnetto 1971*).

Areoligera cf. **coronata** (O. Wetzel) Lejeune-Carpentier 1938

Pl. 3, fig. 6

1966c *Areoligera* cf. *coronata* (O. Wetzel) Lejeune-Carpentier ; Williams & Downie : 228 ; pl. 25, fig. 5 ; text-fig. 63.

DIMENSIONS. Observed range : cyst body (without operculum) 40 × 45 μ to 60 × 82 μ ; length of processes up to 26 μ. (n = 10).

OCCURRENCE. Lower and Middle Eocene.

PREVIOUS RECORDS. Lower Eocene of the London Basin in southern England (Williams & Downie 1966c ; Downie, Husain & Williams 1971*).

Areoligera medusettiformis (O. Wetzel) Lejeune-Carpentier 1938

Pl. 3, fig. 3

1933 *Hystrichosphaera penicillata* (Ehrenberg) O. Wetzel forma *medusettiformis* O. Wetzel : 41 ; pl. 4, fig. 19.
1938 *Areoligera medusettiformis* (O. Wetzel) Lejeune-Carpentier : B170, text-figs 5, 7.

DIMENSIONS. Observed range : cyst body (without operculum) 45 × 48 μ to 60 × 66 μ ; length of processes up to 16 μ. (n = 5).

OCCURRENCE. Lower Eocene.

PREVIOUS RECORDS. Upper Cretaceous (Senonian) of north Germany (O. Wetzel 1933) and of Belgium (Lejeune-Carpentier 1938) ; Cretaceous/Tertiary boundary (Maastrichtian–Danian) of Belgium (Wilson 1971, as *Areoligera senonensis* – pl. 3, fig. 8 only) ; Lower Palaeocene (Danian) of Denmark (Morgenroth 1968, as *A. coronata*) ; Middle Eocene of northern France (Gruas-Cavagnetto 1971*).

***Areoligera* cf. *medusettiformis* (O. Wetzel) Lejeune-Carpentier 1938**

Pl. 3, fig. 7

1966c *Areoligera* cf. *medusettiformis* (O. Wetzel) Lejeune-Carpentier; Williams & Downie: 229; pl. 25, fig. 4.

Dimensions. Observed range: cyst body (without operculum) 40 × 42 μ to 66 × 80 μ; length of processes up to 30 μ. (n = 10).

Occurrence. Lower and Middle Eocene.

Previous Records. Lower Eocene of northern Spain (Caro 1973) and of the London Basin in southern England (Williams & Downie 1966c).

***Areoligera sentosa* n. sp.**

Fig. 8A; Pl. 4, figs 1–2; Pl. 5, figs 1, 3

Derivation of Name. Latin, *sentosus*, thorny or spiny, with reference to the spiny distal margin of the membranes.

Diagnosis. Cyst body dorsoventrally flattened with a smooth or finely granular surface. The circular or subcircular outline may be modified by the development of one or two antapical protuberances. Ventral and dorsal surfaces bear sail-like membranes with incised distal margins which form curved troughs and pointed crests surmounted by erect or curved acuminate spines. Ventral membrane restricted to the peripheral zone, aligned parallel to, and situated close to, the margin of the cyst body. Dorsal membranes organized into process complexes which may be arcuate, soleate or annular on the pre- and postcingular zones, linear on the cingular zone, and annular on the antapical zone. Archaeopyle apical, tetratabular.

Holotype. B.M.(N.H.) Palaeont. slide V.57794 (5). Sample AB40, bed 19, Bracklesham Beds, Upper Eocene, Alum Bay, Isle of Wight, England.

Dimensions. Holotype: cyst body (without operculum) 61 × 77 μ, height of membrane (including spines) up to 25 μ. Observed range: cyst body (without operculum) 52 × 58 μ to 64 × 80 μ, height of membrane (including spines) up to 32 μ. (n = 26).

Remarks. The sail-like membranes have a striated fibrous texture apparently due to the presence of numerous minute fenetrations; they may also show the development of large proximal fenestrations. There is some variation in the type of process complex developed on the dorsal surface. Of the three precingular and three postcingular complexes, in both zones, the middle complex is typically arcuate or soleate, while the other two are soleate or annular. Up to four linear complexes have been observed on the cingular zone; the antapical complex is annular. No forms have been recorded with process complexes developed on the ventral surface. The presence of sail-like membranes and the distinctive form of their distal margins distinguish *Areoligera sentosa* n. sp. from all described species of *Areoligera*.

Occurrence. Middle and Upper Eocene.

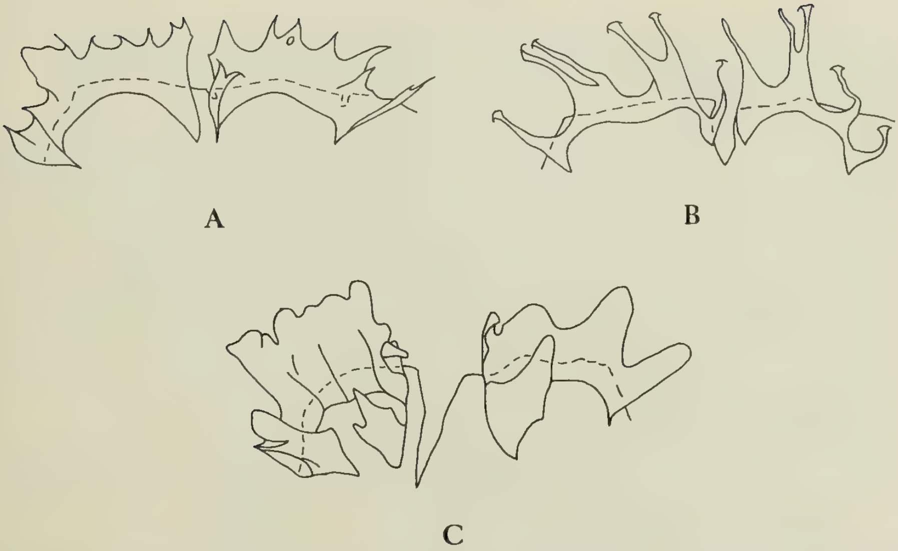


Fig. 8. Process form in three new species of *Areoligera*. A. *Areoligera sentosa* n. sp. V.57767 (2); W56. B. *Areoligera tauloma* n. sp. V.57764 (4); W56. C. *Areoligera undulata* n. sp. V.57800 (2); AB44.

Areoligera tauloma n. sp.

Fig. 8B; Pl. 4, figs 3, 5; Pl. 5, figs 5–6

Derivation of Name. Greek, T, tau cross, *λῶμα*, fringe or border, with reference to the T-shaped terminations of the spines projecting from the distal margin of the membranes.

Diagnosis. Cyst body dorsoventrally flattened with a smooth or finely granular surface. The circular or subcircular outline may be modified by the development of one or two antapical protuberances. Ventral and dorsal surfaces bear sail-like membranes with deeply incised distal margins bearing numerous spines whose distal terminations are generally T-shaped, although a few may be blunt or acuminate. Ventral membrane restricted to the peripheral zone, aligned parallel to, and situated close to, the margin of the cyst body. Dorsal membranes organized into process complexes which may be arcuate, soleate or annular on the pre- and postcingular zones, linear on the cingular zone, and annular on the antapical zone. Archaeopyle apical, tetratabular.

Holotype. B.M.(N.H.) Palaeont. slide V.57768 (3). Sample W57, bed 19c. Bracklesham Beds, Upper Eocene, Whitecliff Bay, Isle of Wight, England.

Dimensions. Holotype: cyst body (without operculum) $59 \times 68\ \mu$; height of membrane (including spines) up to $32\ \mu$. Observed range: cyst body (without operculum) $44 \times 50\ \mu$ to $62 \times 76\ \mu$; height of membrane (including spines) up to $32\ \mu$. ($n = 31$).

Remarks. The textural appearance of the membranes is similar to that of *A. sentosa* n. sp. The T-shaped distal terminations of the spines projecting from the membranes are formed by slightly recurved distal bifurcations, one part being sometimes longer than the other; blunt or acuminate terminations when present are always in a small minority. The variation in the type of process complex developed on the dorsal surface in *A. tauloma* is similar to that shown by *A. sentosa*. When linear complexes are developed on the cingular zone they are restricted to the lateral margins. No forms have been recorded with process complexes developed on the ventral surface. *A. tauloma* is distinguished from *A. sentosa* by having T-shaped terminations on the spinate distal extensions of the membranes. *Cyclonephelium ordinatum* Williams & Downie 1966c has T-shaped distal terminations on its processes, but differs from *A. tauloma* in the distribution, extent and type of process complex development and the overall appearance of its processes.

Occurrence. Middle and Upper Eocene.

Areoligera undulata n. sp.

Figs 8C, 9; Pl. 4, figs 4, 6; Pl. 5, figs 2, 4

1954 *Palmnickia* sp. indet. Eisenack: 70; pl. 12, fig. 20.
1961 *Palmnickia* sp. ex aff. *P. lobifera* Eisenack; Evitt: 400; pl. 8, figs 16–17; pl. 9, figs 8–10.

Derivation of Name. Latin, *undulatus*, wavy, with reference to the undulating nature of the distal margin of the membranes.

Diagnosis. Cyst body dorsoventrally flattened with a smooth of finely granular surface. The circular or subcircular outline may be modified by the development of one or two antapical protuberances. Ventral and dorsal surfaces bear sail-like membranes with lobate undulating distal margins. Ventral membrane restricted to the peripheral zone, aligned parallel to, and situated close to, the margin of the cyst body. Dorsal membranes organized into process complexes which may be arcuate, soleate or annular on the pre- and postcingular zones, linear on the cingular zone, and annular on the antapical zone. Archaeopyle apical, tetratabular.

Holotype. B.M.(N.H.) Palaeont. slide V.57802 (3). Sample AB44, bed 19, Bracklesham Beds, Upper Eocene, Alum Bay, Isle of Wight, England.

Dimensions. Holotype: cyst body (without operculum) $56 \times 82\ \mu$; height of membrane up to $30\ \mu$. Observed range: cyst body (without operculum) $52 \times 54\ \mu$ to $73 \times 92\ \mu$; (complete) $66 \times 68\ \mu$ to $75 \times 75\ \mu$; height of membrane up to $32\ \mu$. (n = 25).

Remarks. A specimen assignable to *Areoligera undulata* n. sp. was recorded from the Upper Eocene of East Prussia by Eisenack (1954), described in the text as *Palmnickia* sp. indet., and on the plate explanation as *Palmnickia* sp. ex aff. *lobifera* (Eisenack 1954: 70; pl. 12, fig. 20). Evitt (1961: 400; pl. 8, figs 16–17; pl. 9, figs 8–10) illustrated and described the specimen recorded by Eisenack, and commented on its affinities with the genus *Areoligera*, noting in particular the overall shape and the distribution of the processes.

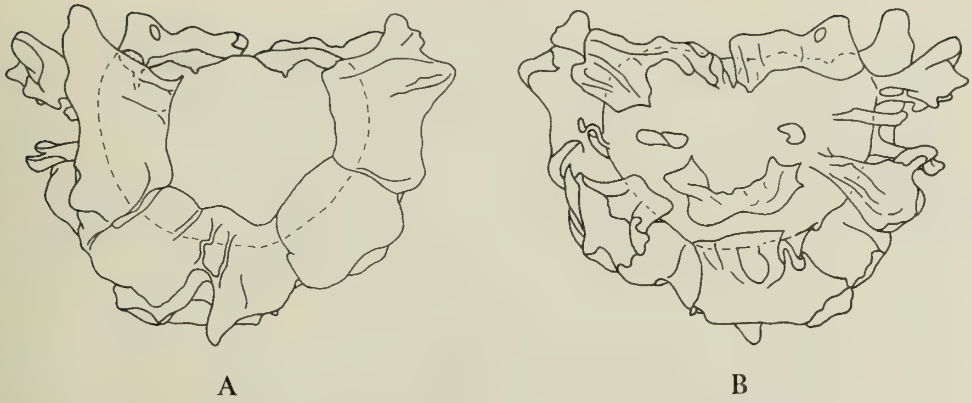


FIG. 9. *Areoligera undulata* n. sp. Holotype. A. Ventral view ; the broken line indicates the margin of cyst body, the apical archaeopyle indicated by shading. B. Dorsal view. V.57802 (3) ; AB44.

The textural appearance of the membranes, and the variation in the type of process complex developed on the dorsal surface in *A. undulata*, are similar to those of *A. sentosa* n. sp. A few specimens have been recorded in which all the pre- and postcingular complexes are annular, while in some forms they are all arcuate. No forms have been recorded with process complexes developed on the ventral surface, although in one specimen there is some loss of proximal continuity in the membrane on the ventral surface. The undulating nature of the distal margin of the sail-like membranes and the absence of distal spines distinguish *A. undulata* from *A. sentosa* n. sp. and *A. tauloma* n. sp.

OCCURRENCE. Middle and Upper Eocene.

PREVIOUS RECORD. Upper Eocene of East Prussia (Eisenack 1954, as *Palmnickia* sp. indet.).

Genus ***AREOSPHAERIDIUM*** Eaton 1971a

The genus and the three species so far assigned to it, mentioned below, have been fully described by Eaton (1971a).

Areosphaeridium diktyoplokus (Klumpp) Eaton 1971a

Pl. 6, fig. 2

1953 *Hystrichosphaeridium diktyoplokus* Klumpp : 392 ; pl. 18, figs 3–7.
1963b *Cordosphaeridium diktyoplokus* (Klumpp) Eisenack : 262 ; pl. 29, fig. 1.
1971a *Areosphaeridium diktyoplokus* (Klumpp) Eaton : 358 ; pl. 1, figs 3–8 ; pl. 2, figs 1–6.

OCCURRENCE. Lower, Middle and Upper Eocene.

PREVIOUS RECORDS. Lower Eocene of Belgium (De Coninck 1972*), of north Germany (Morgenroth 1966a) and of the Hampshire Basin in southern England (Eaton 1971a) ; Middle Eocene of north Germany (Klumpp 1953, Agelopoulos

1967) and of the Hampshire Basin (Eaton 1971a); Upper Eocene of the Aleutian Islands, north Pacific Ocean (Evitt 1970*) including subsurface, offshore (Evitt 1973), of East Prussia (Eisenack 1954), of north Germany (Klumpp 1953, Agelopoulos 1967) and of the Hampshire Basin (Eaton 1971a); Eocene, undifferentiated, of Argentina (Archangelsky 1969*, Archangelsky & Fasola 1971), of Chile (Cookson & Cranwell 1967), of Romania (Balteş 1969) and of the Norwegian North Sea, subsurface, offshore (Jardine & Raynaud 1972); Middle and Upper Oligocene of north Germany (Maier 1959); ? Oligocene of Chile (Archangelsky & Fasola 1971 – indicated as possible reworking); Lower Tertiary, undifferentiated, of Antarctica (in erratics: Cranwell *et al.* 1960 as *Hystrichosphaeridium* sp., Cranwell 1964, McIntyre & Wilson 1966*, Wilson 1967a) and of Tierra del Fuego, Argentina, (Menendez 1965 as *Hystrichosphaeridium dictyostilum*, Baldis 1966); Miocene of Romania (Balteş 1967*). This species has also been recorded as a reworked form in subsurface, offshore glacial sediments of Antarctica (Wilson 1968b) and in the Pleistocene of New Zealand (Wilson 1973).

Areosphaeridium arcuatum Eaton 1971a

Pl. 6, fig. 1

1971a *Areosphaeridium arcuatum* Eaton: 360; pl. 3, figs 1–9; text-figs 4–5.

OCCURRENCE. Middle and Upper Eocene.

PREVIOUS RECORDS. Middle and Upper Eocene of the Hampshire Basin in southern England (Eaton 1971a).

Areosphaeridium multicornutum Eaton 1971a

Pl. 6, fig. 3

1971a *Areosphaeridium multicornutum* Eaton: 363; pl. 4, figs 1–7; text-fig. 6.

OCCURRENCE. Upper Eocene.

PREVIOUS RECORD. Upper Eocene of the Hampshire Basin in southern England (Eaton 1971a).

Genus ***CANNOSPHAEROPSIS*** O. Wetzel 1933 emend. Williams & Downie 1966c

Cannosphaeropsis reticulensis Pastiels 1948

Pl. 2, fig. 4

1948 *Cannosphaeropsis reticulensis* Pastiels: 49; pl. 5, figs 7–10.

DIMENSIONS. Observed range: diameter of cyst body 30–39 μ; length of processes up to 16 μ. (n = 8).

REMARKS. The processes in *C. reticulensis* are sutural and gonal in position, simple or proximally branched, and distally united by slender flexuous trabeculae which occasionally bear acuminate spines. When present, the archaeopyle is precingular in position.

Occurrence. Lower, Middle and Upper Eocene.

Previous Records (not including records of this species attributed to *Adnatosphaeridium*). Palaeocene and Lower Eocene of northern France (Chateauneuf & Gruas-Cavagnetto 1968*); Lower Eocene of Belgium (Pastiels 1948, Morgenroth 1966a – doubtful attribution), of the Hampshire Basin (Williams & Downie 1966c) and of the London Basin in southern England (Williams & Downie 1966c, Gruas-Cavagnetto 1970c*); Upper Eocene of north Germany (Alberti 1961); Upper Eocene, Lower and Middle Oligocene of Northern France (Chateauneuf & Gruas-Cavagnetto 1968*).

Genus ***CHIROPTERIDIUM*** Gocht 1960

Chiropteridium cf. ***dispersum*** Gocht 1960

Fig. 10; Pl. 7, fig. 4

Description. Cyst body dorsoventrally flattened with a finely granular surface. The circular or subcircular outline may be modified by the development of one or two antapical protuberances. Sail-like membranous processes are present on the ventral and dorsal surfaces; they are arcuate in cross-section, variable in breadth, and frequently exhibit large fenestrations. The processes are finely striated and have a pseudo-fibrous appearance and their distal margins vary from entire to deeply incised. The distal terminations may be digitate, secate or acuminate. The majority of the processes are concentrated on the peripheral zone of the cyst body, where they are arranged in two rows, one on the ventral and the other on the dorsal surface. The rows are close to, and approximately parallel to, the margin of the

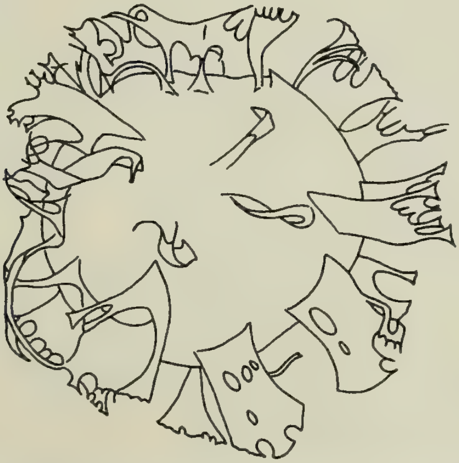


Fig. 10. *Chiropteridium* cf. *dispersum* Gocht 1960. Complete specimen characteristically showing the majority of the processes concentrated on the peripheral zone of the dorsoventrally flattened cyst body. V.57753 (3); W38.

cyst body. Processes are also present on the mid-ventral and mid-dorsal areas. They are sparsely distributed and show a variation in form similar to that of the processes on the peripheral zone. Archaeopyle apical, tetratabular.

DIMENSIONS. Observed range: cyst body $31 \times 37\ \mu$ to $58 \times 54\ \mu$; length of processes up to $26\ \mu$. (n = 16).

REMARKS. The specimens assigned to *C.* cf. *dispersum* are similar to *C. dispersum* Gocht 1960 in overall form, but differ in having fewer additional processes on the mid-dorsal and mid-ventral areas, and a smaller proportion of distally deeply incised processes on the peripheral zone.

OCCURRENCE. Lower and Middle Eocene.

Genus ***CORDOSPHAERIDIUM*** Eisenack 1963b emend. Morgenroth 1968

Cordosphaeridium inodes (Klumpp) Eisenack 1963b emend. Morgenroth 1968

Pl. 6, fig. 5

1953 *Hystrichosphaeridium inodes* Klumpp: 391; pl. 18, figs 1–2.
1963b *Cordosphaeridium inodes* (Klumpp) Eisenack: 261; pl. 29, fig. 3.
1968 *Cordosphaeridium inodes* (Klumpp) Eisenack emend. Morgenroth: 549; pl. 46, figs 1–8; not pl. 45, fig. 9.

DIMENSIONS. Observed range: diameter of cyst body $39–50\ \mu$; length of processes up to $20\ \mu$. (n = 11).

OCCURRENCE. Lower, Middle and Upper Eocene.

PREVIOUS RECORDS. Lower Palaeocene (Danian) of California, U.S.A. (Drugg 1967) and of Denmark (Morgenroth 1968); Palaeocene of northern France (Chateauneuf & Gruas-Cavagnetto 1968), of northern Spain (Caro 1973 – doubtful attribution), of Tasmania (Cookson & Eisenack 1967a – doubtful attribution) and of Victoria, Australia (Cookson & Eisenack 1967b); Lower Eocene of Belgium (De Coninck 1965, 1967*, 1968, Morgenroth 1966a), of northern France (Chateauneuf & Gruas-Cavagnetto 1968, Gruas-Cavagnetto 1968, 1970b), of north Germany (Morgenroth 1966a, Gocht 1969), of northern Spain (Caro 1973 – doubtful attribution), of the Hampshire and London Basins in southern England (Davey & Williams 1966b, Downie, Husain & Williams 1971*), and of Victoria, Australia (Deflandre & Cookson 1955); Middle Eocene of northern France (Gruas-Cavagnetto 1971*), of north Germany (Klumpp 1953, Agelopoulos 1967, Gocht 1969) and of the Hampshire Basin (Gruas-Cavagnetto 1970a*); Upper Eocene of Belgium (Rozen 1965), of north Germany (Klumpp 1953, Agelopoulos 1967) and of the Hampshire Basin (Gruas-Cavagnetto 1970a*); ? Upper Eocene of north Germany (Gocht 1969); Eocene, undifferentiated, of Victoria, Australia (Deflandre & Cookson 1955); Middle Oligocene of north Germany (Gerlach 1961, Gocht 1969, Benedek 1972) and of the Hampshire Basin (Gruas-Cavagnetto 1970a*); Upper Oligocene of north Germany (Gerlach 1961, Brosius 1963, Benedek 1972); Oligocene, undifferentiated, of Victoria (Cookson 1953, as *Hystrichosphaeridium truncigerum*); Middle Miocene of north Germany (Gerlach 1961).

Cordosphaeridium exilimurum Davey & Williams 1966b

Pl. 6, fig. 8

1966b *Cordosphaeridium exilimurum* Davey & Williams : 87 ; pl. 11, fig. 2.

DIMENSIONS. Observed range : diameter of cyst body 45–65 μ ; processes, length up to 30 μ, breadth up to 30 μ. (n = 8).

REMARKS. The processes are frequently broad, and typically fenestrate. The specimens here attributed to this species indicate that the archaeopyle is precingular in position, and not apical as stated by Davey & Williams (1966b).

OCCURRENCE. Lower, Middle and Upper Eocene.

PREVIOUS RECORDS. Lower Eocene of the Hampshire and London Basins in southern England (Davey & Williams 1966b, Downie, Husain & Williams 1971*).

Cordosphaeridium fibrospinosum Davey & Williams 1966b

Pl. 6, fig. 6

1966b *Cordosphaeridium fibrospinosum* Davey & Williams : 86 ; pl. 5, fig. 5.

DIMENSIONS. Observed range : diameter of cyst body 40–70 μ ; processes, length up to 15 μ, breadth up to 26 μ. (n = 6).

REMARKS. The specimens here attributed to this species, and those recorded by Gocht (1969), indicate that the archaeopyle is precingular in position and not apical as stated by Davey & Williams (1966b).

OCCURRENCE. Lower and Middle Eocene.

PREVIOUS RECORDS. Upper Cretaceous (Senonian) of Natal, South Africa (Davey 1969b) ; Palaeocene of north Germany (Gocht 1969) and of northern Spain (Caro 1973) ; Lower Eocene of north Germany (Gocht 1969) and of the Hampshire and London Basins in southern England (Davey & Williams 1966b, Downie, Husain & Williams 1971*) ; Middle Eocene of north Germany (Gocht 1969) and of northern France (Gruas-Cavagnetto 1971*) ; ? Upper Eocene of north Germany (Gocht 1969) ; Middle and Upper Oligocene of north Germany (Benedek 1972).

Cordosphaeridium gracilis (Eisenack) Davey & Williams 1966b

Pl. 6, fig. 7

1954 *Hystrichosphaeridium inodes* Klumpp subsp. *gracilis* Eisenack : 66 ; pl. 8, fig. 17 ; pl. 10, figs 3–8 ; pl. 12, figs 7, 21.

1963b *Cordosphaeridium inodes* (Klumpp) Eisenack subsp. *gracilis* (Eisenack) Eisenack : 261 ; pl. 29, fig. 2.

1966b *Cordosphaeridium gracilis* (Eisenack) Davey & Williams : 84 ; pl. 3, fig. 8 ; pl. 11, figs 4, 6–7 ; text-fig. 19.

DIMENSIONS. Observed range : diameter of cyst body 53–72 μ ; length of processes up to 52 μ. (n = 13).

REMARKS. The slender processes are simple or branched ; when branched they are distinctly Y-shaped.

OCCURRENCE. Lower, Middle and Upper Eocene.

PREVIOUS RECORDS. Lower Eocene of Belgium (Pastiels 1948, as *Hystrichosphaeridium tubiferum* ; Morgenroth 1966a), of northern France (Gruas-Cavagnetto 1970b*), of north Germany (Morgenroth 1966a, Gocht 1969) and of the Hampshire and London Basins in southern England (Davey & Williams 1966b ; Downie, Husain & Williams 1971) ; Middle Eocene of northern France (Gruas-Cavagnetto 1971*) and of north Germany (Agelopoulos 1967, Gocht 1969) ; Upper Eocene of East Prussia (Eisenack 1938, as *Hystrichosphaera* cf. *ramosa* ; Eisenack 1954), of north Germany (Agelopoulos 1967) and of the Hampshire Basin (Gruas-Cavagnetto 1970a*) ; ? Upper Eocene of north Germany (Gocht 1969) ; Middle Oligocene of north Germany (Gerlach 1961, Gocht 1969, Benedek 1972) ; Upper Oligocene of north Germany (Benedek 1972) ; Middle Miocene of north Germany (Gerlach 1961).

Cordosphaeridium ? minimum (Morgenroth) Benedek 1972

Pl. 7, figs 1–3

1966a *Cordosphaeridium inodes* Klumpp subsp. *minimum* Morgenroth : 24 ; pl. 5, figs 6–7.
1972 *Cordosphaeridium minimum* (Morgenroth) Benedek : 25 ; pl. 9, fig. 3 ; text-fig. 8.

DIMENSIONS. Observed range : diameter of cyst body 18–28 μ ; length of processes up to 12 μ. (n = 10).

REMARKS. This species is here questionably assigned to *Cordosphaeridium*. The thin-walled, distally expanded processes have numerous thickened ribs which extend to the distal margin ; their overall appearance is not comparable to the typical fibrous appearance of the processes in *Cordosphaeridium*. The process ribs usually extend onto the surface of the cyst body where they intersect to form a complex system of polygonal fields. The position of the archaeopyle is uncertain, but the specimens here recorded show some indication that it may possibly be apical in position. Morgenroth (1966a) recorded one specimen showing an elliptical opening, while Benedek (1972) did not observe any significant openings.

OCCURRENCE. Middle and Upper Eocene.

PREVIOUS RECORDS. Lower Eocene of north Germany (Morgenroth 1966a) ; Middle Oligocene of north Germany (Benedek 1972).

Cordosphaeridium multispinosum Davey & Williams 1966b

Pl. 6, fig. 4

1966b *Cordosphaeridium multispinosum* Davey & Williams : 89 ; pl. 3, fig. 6.

DIMENSIONS. Observed range : diameter of cyst body 42–60 μ ; length of processes up to 18 μ. (n = 10).

REMARKS. The numerous short fibrous processes in *C. multispinosum* have a delicate appearance, are simple or branched, occasionally proximally united, and usually slightly expanded distally.

OCCURRENCE. Lower and Middle Eocene.

PREVIOUS RECORDS. Lower Eocene of Belgium (De Coninck 1972*), of northern France (Gruas-Cavagnetto 1968, Chateauneuf & Gruas-Cavagnetto 1968*) and of the Hampshire and London Basins in southern England (Davey & Williams 1966b) ; Middle Eocene of northern France (Gruas-Cavagnetto 1971*).

Genus ***CYCLONEPHELIUM*** Deflandre & Cookson 1955
emend. Williams & Downie 1966c

Cyclonephelium divaricatum Williams & Downie 1966c

Pl. 7, fig. 5

1966c *Cyclonephelium divaricatum* Williams & Downie : 223 ; pl. 25, fig. 1 ; text-fig. 60.

DIMENSIONS. Observed range : cyst body (without operculum) $42 \times 48\ \mu$ to $66 \times 68\ \mu$; length of processes up to $21\ \mu$. ($n = 11$).

REMARKS. Characterized by the presence of distal spines and secae arising from the trabeculae or perforated membranes which complexly unite the processes.

OCCURRENCE. Lower and Middle Eocene.

PREVIOUS RECORDS. Lower Eocene of the Hampshire and London Basins in southern England (Williams & Downie 1966c, Downie, Husain & Williams 1971*) ; Middle Eocene of northern France (Gruas-Cavagnetto 1971*).

Cyclonephelium exuberans Deflandre & Cookson 1955

Pl. 8, figs 1–2

1948 *Membranilarnax pterospermoides* O. Wetzel ; Pastiels : 46 ; pl. 5, figs 11, 13–14 ; not fig. 12.
1955 *Cyclonephelium exuberans* Deflandre & Cookson : 285 (nom. nud.).
1966c *Cyclonephelium exuberans* Deflandre & Cookson ; Williams & Downie : 225 (in part) ; not text-fig. 61.
1973 *Cyclonephelium pastielsi* Deflandre & Cookson ; Caro : 352 (in part) ; pl. 1, fig. 8.

DIAGNOSIS. Cyst body dorsoventrally flattened with a smooth or finely granular surface. The circular or subcircular outline may be modified by the development of one or two antapical protuberances. Processes restricted to the peripheral zone of the cyst body ; variable in breadth and simple or branched, distally complexly united by trabeculae and areas of variably fenestrate membrane. No processes developed on reflected precingular plates 3″ and 6″. Archaeopyle apical, tetratabular.

HOLOTYPE. The specimen figured as *Membranilarnax pterospermoides* O. Wetzel 1933 by Pastiels (1948 : pl. 5, figs 11, 13) ; Lower Eocene, Quenast, Belgium.

DIMENSIONS. Holotype: cyst body (without operculum) 29 × 39 μ; length of processes up to 25 μ. Observed range (this study): cyst body 54 × 50 μ to 80 × 80 μ; length of processes up to 38 μ. (n = 26).

REMARKS. Deflandre & Cookson (1955 : 285) applied the name *Cyclonephelium exuberans* as a new species to forms described from the Lower Eocene of Belgium by Pastiels (1948) as *Membranilarnax pterospermoides* O. Wetzel 1933. However, no holotype was designated, thus rendering the species invalid under Art. 37 of the I.C.B.N. To rectify this point one of the specimens illustrated by Pastiels (1948 : pl. 5, figs 11, 13) is here designated as holotype, and a diagnosis given. Pastiels provided four illustrations of *M. pterospermoides* (Pastiels 1948 : pl. 5, figs 11–14). The concept of *C. exuberans* is here restricted to forms similar to the specimen represented by a photograph in Pastiels (1948 : pl. 5, fig. 11), and a probable camera lucida drawing (pl. 5, fig. 13). A diagrammatic representation of the same specimen, which is devoid of processes on reflected precingular plates 3″ and 6″, is given in pl. 5, fig. 14. Other specimens, similar to that illustrated by Pastiels (1948 : pl. 5, fig. 12) with processes developed on all the precingular plates, are here assigned to *C.* aff. *exuberans*.

OCCURRENCE. Lower, Middle and Upper Eocene.

PREVIOUS RECORDS. Palaeocene and Lower Eocene of northern Spain (Caro 1973, as *C. pastielsi* in part); Lower Eocene of Belgium (Pastiels 1948, as *M. pterospermoides*, pl. 5, figs 11, 13–14 only; De Coninck 1967*, 1972*) and of the Hampshire and London Basins in southern England (Williams & Downie 1966c, in part, not text-fig. 61; Downie, Husain & Williams 1971*).

***Cyclonephelium* aff. *exuberans* Deflandre & Cookson 1955 *ex* Eaton 1976**

Pl. 7, fig. 7

1948 *Membranilarnax pterospermoides* O. Wetzel; Pastiels: 46; pl. 15, fig. 12; not figs 11, 13–14.
1966c *Cyclonephelium exuberans* Deflandre & Cookson; Williams & Downie: 225 (in part); text-fig. 61.
1966c *Cyclonephelium pastielsi* Deflandre & Cookson; Williams & Downie: 227; pl. 25, fig. 2.
1969 *Cyclonephelium pastielsi* Deflandre & Cookson; Gocht: 60; pl. 8, fig. 15.
1971 *Cyclonephelium pastielsi* Deflandre & Cookson; Downie, Husain & Williams: pl. 1, fig. 12.
1972 *Cyclonephelium exuberans* Deflandre & Cookson; Benedek: 8; pl. 1, fig. 5.
1973 *Cyclonephelium pastielsi* Deflandre & Cookson; Caro: 352 (in part); not pl. 1, fig. 8.

DIMENSIONS. Observed range: cyst body 54 × 54 μ to 75 × 80 μ; length of processes up to 40 μ. (n = 5).

REMARKS. In the shape and surface ornamentation of the cyst body, the form of the processes and the complex development of distal trabeculae and variably fenestrate membrane, *C.* aff. *exuberans* is very similar to *C. exuberans*, but is distinguished in usually having processes developed on all six reflected precingular plates. The processes on reflected plates 3″ and 6″ may be reduced in size, and in some specimens one of these two plates (but never both) may be devoid of processes. Although the forms here described as *C. exuberans* and *C.* aff. *exuberans* were originally considered to represent one species (Pastiels' concept of *M. pterospermoides* O. Wetzel 1933), the separation of the two was found to be of palynostratigraphical significance.

Occurrence. Lower Eocene.

Previous Records. Palaeocene and Lower Eocene of northern Spain (Caro 1973, as *C. pastielsi* in part ; not pl. 1, fig. 8) ; Lower Eocene of Belgium (Pastiels 1948, as *M. pterospermoides*, pl. 5, fig. 12 only ; De Coninck 1965, questionably as *C. exuberans* ; Morgenroth 1966a, questionably as *C. pastielsi*), of north Germany (Gocht 1969, as *C. pastielsi*) and of the Hampshire and London Basins in southern England (Williams & Downie 1966c, as *C. exuberans* in part and *C. pastielsi* ; Downie, Husain & Williams 1971, as *C. pastielsi*) ; Middle and Upper Oligocene of north Germany (Benedek 1972, as *C. exuberans*).

Cyclonephelium intricatum Eaton 1971a

Pl. 8, fig. 6

1971a *Cyclonephelium intricatum* Eaton : 365 ; pl. 4, figs 8–10.

Occurrence. Middle and Upper Eocene.

Previous Records. Middle and Upper Eocene of the Hampshire Basin (Eaton 1971a) ; Upper Oligocene of north Germany (Brosius 1963, questionably as *C. reticulosum*).

Cyclonephelium laciniiforme Gerlach 1961

Fig. 11 ; Pl. 7, fig. 6

1961 *Cyclonephelium laciniiforme* Gerlach : 206 ; pl. 29, fig. 4.

Description. Cyst body dorsoventrally flattened with a subcircular outline, and a smooth or finely granular surface. Processes restricted to the peripheral zone of the cyst body, membranous and roughly T-shaped in overall form. Distally the processes are expanded, the majority united by membranous trabeculae of variable width. Archaeopyle apical, tetratabular.

Dimensions. Observed range : cyst body (without operculum) $42 \times 42\ \mu$ to $58 \times 66\ \mu$; length of processes up to $30\ \mu$. ($n = 10$).

Occurrence. Lower, Middle and Upper Eocene.

Previous Records. Middle Oligocene of north Germany (Gerlach 1961 ; Benedek 1972, doubtful attribution) ; Upper Oligocene of north Germany (Brosius 1963 ; Benedek 1972, doubtful attribution) ; ? Upper Oligocene of north Germany (Gerlach 1961).

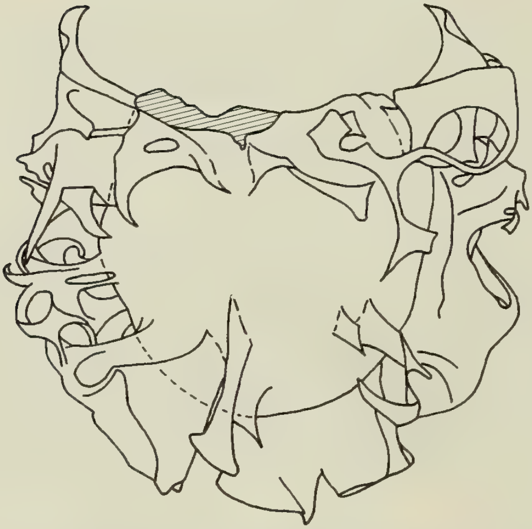


FIG. 11. *Cyclonephelium laciniiforme* Gerlach 1961. The apical archaeopyle is indicated by shading. V.57756 (8); W40.

Cyclonephelium ordinatum Williams & Downie 1966c

Pl. 7, fig. 8

1966c *Cyclonephelium ordinatum* Williams & Downie : 225 ; pl. 25, fig. 3 ; text-fig. 62.

DIMENSIONS. Observed range: cyst body 50 × 52 μ to 68 × 75 μ; length of processes up to 30 μ. (n = 9).

REMARKS. The processes are similar to those of several members of the *Areoligera senonensis* complex (*A. coronata, A.* cf. *coronata, A. medusettiformis* and *A.* cf. *medusettiformis*). It also resembles *Areoligera* in having its processes organized into process complexes; however, only linear and occasionally arcuate complexes are developed, and the processes are restricted to the peripheral zone of the cyst body.

OCCURRENCE. Lower and Middle Eocene.

PREVIOUS RECORDS. Palaeocene of northern Spain (Caro 1973); Lower Eocene of north Germany (Gocht 1969), of northern Spain (Caro 1973) and of the Hampshire and London Basins in southern England (Williams & Downie 1966c, Downie, Husain & Williams 1971*); Middle Eocene of northern France (Gruas-Cavagnetto 1971*) and north Germany (Gocht 1969); Middle Oligocene of north Germany (Benedek 1972, doubtful attribution).

Cyclonephelium pastielsi Deflandre & Cookson 1955

1948 *Membranilarnax* cf. *liradiscoides* O. Wetzel; Pastiels : 47 ; pl. 5, fig. 15.
1955 *Cyclonephelium pastielsi* Deflandre & Cookson : 285 (nom. nud.).

1965 *Cyclonephelium pastielsi* Deflandre & Cookson ; De Coninck : 44 ; pl. 12, figs 32, 35, 39.
1968 *Cyclonephelium pastielsi* Deflandre & Cookson ; Gruas-Cavagnetto : 83 ; pl. 12, fig. 4 ; pl. 16, fig. 14.
1968 *Cyclonephelium pastielsi* Deflandre & Cookson ; De Coninck : 41 ; pl. 12, figs 10–11, 15–16.
1970 *Cyclonephelium pastielsi* Deflandre & Cookson ; Gruas-Cavagnetto : pl. 2, fig. 4.

DIAGNOSIS. See description of *Membranilarnax* cf. *liradiscoides* O. Wetzel 1933 by Pastiels (1948 : 47).

HOLOTYPE. The specimen figured as *Membranilarnax* cf. *liradiscoides* O. Wetzel 1933 by Pastiels (1948 : pl. 5, fig. 15) ; Lower Eocene, Quenast, Belgium.

DIMENSIONS. Holotype : cyst body (without operculum) $53 \times 57\ \mu$; length of processes up to $30\ \mu$.

REMARKS. As in the case of *Cyclonephelium exuberans*, Deflandre & Cookson (1955 : 285) also failed to designate a holotype for *Cyclonephelium pastielsi*, their new species name for forms described from the Lower Eocene of Belgium by Pastiels (1948) as *Membranilarnax* cf. *liradiscoides* O. Wetzel 1933. However, since he only provided one illustration of *M.* cf. *liradiscoides* (Pastiels 1948 : pl. 5, fig. 15, a probable camera lucida drawing) this must be the holotype, and it is here designated as such. Pastiels' original description of this form (1948 : 47) indicates that it consists of a central body with processes restricted to the peripheral zone. The processes are simple or bifurcate, distally ramified and interconnected, and the illustrated specimen is devoid of them on reflected precingular plates 3″ and 6″. In overall form the specimen illustrated by Pastiels is more closely comparable to *Cyclonephelium retiintextum* Cookson 1965 (De Coninck 1968 : 41) than *C. exuberans* (Williams & Downie 1966c : 225, 227). On this basis, *C. pastielsi* can only be considered to have been recorded from the Lower Eocene of Belgium (Pastiels 1948, as *M.* cf. *liradiscoides* ; De Coninck 1965, 1968, Gruas-Cavagnetto 1968) and of northern France (Gruas-Cavagnetto 1968, 1970b). There are also several listed records without illustration or description which cannot be commented on : Lower Eocene of Belgium (De Coninck 1967), of northern France (Chateauneuf & Gruas-Cavagnetto 1968) and of the Hampshire Basin in southern England (Gruas-Cavagnetto 1970a) ; Middle Eocene of northern France (Gruas-Cavagnetto 1971).

Cyclonephelium spinetum n. sp.

Fig. 12 ; Pl. 8, fig. 3

DERIVATION OF NAME. Latin, *spinetum*, thorn-hedge, with reference to the appearance of the spine-bearing distal trabeculae.

DIAGNOSIS. Cyst body dorsoventrally flattened with a smooth or finely granular surface. The circular or subcircular outline may be modified by the development of an antapical protuberance. Processes, restricted to the peripheral zone of the cyst body, broad and membranous, and distally expanded and united by membranous, arched trabeculae of variable width which bear numerous acuminate spines. Archaeopyle apical, tetratabular.

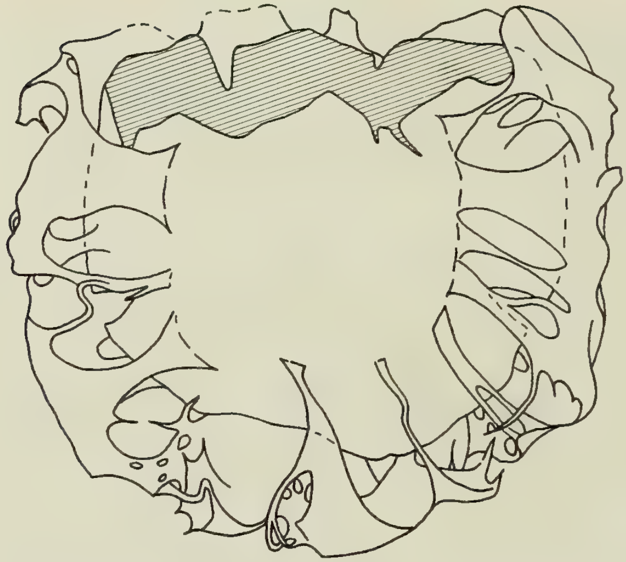


FIG. 12. *Cyclonephelium spinetum* n. sp. Holotype; the apical archaeopyle is indicated by shading. V.57742; W26A.

HOLOTYPE. B.M.(N.H.) Palaeont. slide V.57742. Sample W26A, bed 9a, Bracklesham Beds, Lower Eocene, Whitecliff Bay, Isle of Wight, England.

DIMENSIONS. Holotype: cyst body (without operculum) 55 × 65 μ; length of processes up to 22 μ. Observed range: cyst body (without operculum) 40 × 55 μ to 58 × 68 μ; length of processes up to 36 μ. (n = 10).

REMARKS. The membranous processes are smooth or finely striated. They show considerable variation in breadth, varying from very broad and proximally closely spaced to narrow and proximally widely spaced. The overall form of the processes is broadly T-shaped. The acuminate spines projecting from the distal trabeculae show considerable variation in length, while the trabeculae themselves vary from broad and ribbon-like to slender strands. *Cyclonephelium spinetum* n. sp. is similar to *C. laciniiforme* Gerlach 1961 in overall form, but differs in having numerous acuminate spines projecting from the distal trabeculae. Acuminate spines are also developed in *C. divaricatum* Williams & Downie 1966c, but this species does not have the broad membranous processes which are typical of *C. spinetum*.

OCCURRENCE. Lower and Middle Eocene.

Cyclonephelium vicinum n. sp.

Fig. 13; Pl. 8, figs 4–5

DERIVATION OF NAME. Latin, *vicinus*, near or neighbouring, with reference to the periphragm which remains close to the endophragm where the two layers are separated.

Diagnosis. Cyst body dorsoventrally flattened with a circular or subcircular outline. The finely granular periphragm is separated from, but remains close to, the endophragm over the peripheral zone of the cyst body. The separated periphragm is wrinkled and folded. Fenestrations may be developed adjacent to, or sometimes away from, the line of separation. Archaeopyle apical, tetratabular.

Holotype. B.M.(N.H.) Palaeont. slide V.57744. Sample W26A, bed 9a, Bracklesham Beds, Lower Eocene, Whitecliff Bay, Isle of Wight, England.

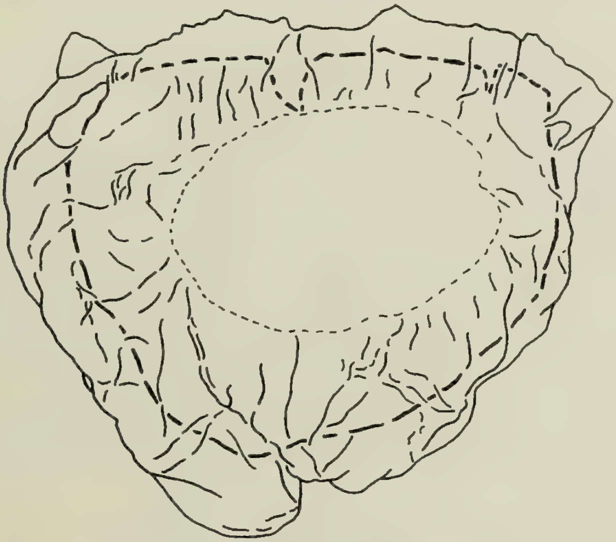


Fig. 13. *Cyclonephelium vicinum* n. sp. Holotype, showing the characteristic wrinkling and folding in the periphragm where it is separated from the endophragm. V.57744; W26A.

Dimensions. Holotype: cyst body (without operculum) 54 × 67 μ; height of pericoel up to 14 μ. Observed range: cyst body (without operculum) 45 × 50 μ to 68 × 77 μ; height of pericoel up to 18 μ. (n = 18).

Remarks. The development of several fenestrations in the separated periphragm adjacent to the line of separation may give the appearance of a row of distally united membranous processes. The presence of a marginal pericoel distinguishes *C. vicinum* n. sp. from all described species of *Cyclonephelium.* In overall form the specimens here described are similar to those recorded from the Middle Oligocene of north Germany by Gocht (1969) as *Chiropteridium aspinatum* (Gerlach) Brosius 1963, but in *C. vicinum* the separated periphragm usually lies closer to the endophragm. The assignment of Gocht's specimens to *Chiropteridium* seems questionable, and it is possible that *C. vicinum* may be an evolutionary predecessor of the forms described by Gocht. This problem cannot be resolved until forms of intermediate age have been studied.

Occurrence. Lower, Middle and Upper Eocene.

Genus ***DIPHYES*** Cookson 1965 emend. Davey & Williams 1966b

Diphyes colligerum (Deflandre & Cookson) Cookson 1965 emend. Davey & Williams 1966b

Pl. 8, fig. 7

1955 *Hystrichosphaeridium colligerum* Deflandre & Cookson : 178 ; pl. 7, fig. 3.
1965 *Diphyes colligerum* (Deflandre & Cookson) Cookson : 86 ; pl. 9, figs 1–12.
1966b *Diphyes colligerum* (Deflandre & Cookson) Cookson emend. Davey & Williams : 96 ; pl. 4, figs 2–3.

Dimensions. Observed range : diameter of cyst body 24–40 μ ; length of slender processes up to 20 μ ; length of antapical process up to 20 μ. (n = 15).

Occurrence. Lower, Middle and Upper Eocene.

Previous Records. Questionably from the Upper Cretaceous, probable Senonian, of Victoria, Australia (Cookson 1965) ; Palaeocene of South Dakota, U.S.A. (Stanley 1965), of Tasmania (Cookson & Eisenack 1967a), of Victoria (Cookson & Eisenack 1967b) and of France (Chateauneuf & Gruas-Cavagnetto 1968) ; Lower Eocene of Belgium (Morgenroth 1966a, De Coninck 1968), of northern France (Gruas-Cavagnetto 1968, 1970b*, Chateauneuf & Gruas-Cavagnetto 1968), of north Germany (Morgenroth 1966a), of the Hampshire and London Basins in southern England (Davey & Williams 1966b) and of Victoria (Deflandre & Cookson 1955) ; Middle Eocene of northern France (Gruas-Cavagnetto 1971*) ; Upper Eocene of Belgium (Rozen 1965), of Victoria (Cookson 1965) and of the Aleutian Islands, north Pacific Ocean (Evitt 1970*) ; Eocene, undifferentiated, of Western Australia (Cookson & Eisenack 1961) ; ? Oligocene of Victoria (Cookson 1953, as *Hystrichosphaeridium* sp. c).

Genus ***DISTATODINIUM*** nov.

Derivation of Name. Latin, *distatus*, differed, stood apart, with reference to the distinctive form of the processes.

Diagnosis. Dinoflagellate cysts in which the cyst body has an oval or elongate oval outline. Processes simple or branched, variable in breadth, flattened and blade-like in cross-section, proximally expanded and frequently united by a membrane, distally expanded and ramified. Ramifications typically, but not invariably, complex. Occasionally, slender tubular processes are present. The number of processes varies from about 14 (in some specimens without an operculum) to about 60 or more. Processes aligned into rows parallel to the long axis of the cyst body, and apparently situated on or close to reflected plate boundaries ; many are also arranged in a more or less circular manner around the cyst body. Archaeopyle apical.

Type Species. *Distatodinium craterum* gen. et sp. nov., Bracklesham Beds, Upper Eocene, Isle of Wight, England.

Remarks. Three features suggest that the processes in *Distatodinium* gen. nov. are basically sutural in position, their distribution pattern over the cyst body, the occasional presence of processes which are T-shaped in cross-section and probably gonal in position and the occurrence of proximal membrane uniting processes across reflected tabulation zone boundaries. However, in some specimens of *D. ellipticum* (Cookson 1965) n. comb., processes are present which cannot be interpreted as sutural, and some are arranged in arcuate complexes. The reflected tabulation of *Distatodinium* has not been determined, but process distribution in *D. craterum* n. sp. suggests there are six precingular and at least five postcingular plates. The majority of the flattened blade-like processes appear to be solid, particularly in the proximal region. This is emphasized by a straight or curved line at the base of the processes, marking their divergence from the cyst body. There is some indication that the distal ramifications may be hollow, and some very slender tubular processes have been observed. Two described genera, *Prolixosphaeridium* Davey *et al.* 1966b and *Tanyosphaeridium* Davey & Williams 1966b, are comparable to *Distatodinium* in having an elongate cyst body and an apical archeopyle. In *Prolixosphaeridium* the distribution of the processes may be similar to *Distatodinium*, but they are distally less complex, being not obviously blade-like in cross-section or proximally united by membrane. In *Tanyosphaeridium* the processes are again distally less complex, and they are considered to be intratabular in distribution. They are also cylindrical, and circular or subcircular in cross-section.

In addition to the species assigned to *Distatodinium* and described in this paper, one other species is also transferred to the genus. This is *Distatodinium tenerum* (Benedek 1972) n. comb. = *Tanyosphaeridium tenerum* Benedek 1972 : 35 ; pl. 10, figs 13–14 ; text-fig. 14. Middle Oligocene, north Germany.

Distatodinium craterum n. sp.

Pl. 9, figs 1–5

1961 *Hystrichosphaeridea* Scherer : fig. 2.

Derivation of Name. Greek κρᾰτερός, strong, with reference to the appearance of the broad processes.

Diagnosis. The cyst body has an elongate oval outline and a smooth or finely granular surface. The processes are typically broad, simple or branched, flattened and blade-like in cross-section, distally and proximally expanded. Distally they are bifurcate or trifurcate with complex secondary and tertiary branchlets, the ramifications having a twig-like appearance. Typically 13 to 17 processes on specimens which have lost the operculum ; there are six processes on the precingular and five on the postcingular zone. Cingular zone devoid of processes. Usually one, sometimes two processes at the antapical pole. Between one and four additional processes may be present, apparently intermediate in position between the primary postcingular and antapical processes. The processes are also arranged into six rows parallel to the long axis of the cyst body. The straight or curved lines marking the divergence of the processes from the cyst body are also parallel to the long axis. Adjacent longitudinally aligned processes may be proximally united by membrane. Archaeopyle apical.

Holotype. B.M.(N.H.) Palaeont. slide V.57792. Sample AB40, bed 19, Bracklesham Beds, Upper Eocene, Alum Bay, Isle of Wight, England.

Dimensions. Holotype: cyst body (without operculum) $44 \times 30\ \mu$; processes, length up to 22 μ, breadth up to 7 μ. Observed range: cyst body (without operculum) $35 \times 20\ \mu$ to $55 \times 38\ \mu$; processes, length up to 30 μ, maximum breadth 5–11 μ. (n = 25).

Remarks. No detached or in place opercula have been observed in *D. craterum* n. sp. The observed maximum number of processes is 17, but in the majority of specimens there are 14. The flattening and alignment of the processes parallel to the long axis of the cyst body, and the development of membrane proximally uniting longitudinally aligned processes in separate reflected tabulation zones, strongly suggest that the processes are sutural in position. This would indicate the presence of six precingular plates and at least five postcingular plates. *D. craterum* is distinguished from all described species here attributed to *Distatodinium* by the overall broader and stronger form of its processes. It is further distinguished from *D. ellipticum* (Cookson 1965) n. comb. by having considerably fewer processes (about 14 as opposed to about 40 or more in *D. ellipticum*), and from *D. tenerum* (Benedek 1972) n. comb. by again having considerably fewer processes which are longer, and distally more complex.

Occurrence. Upper Eocene.

Previous Record. Middle Oligocene of Switzerland (Scherer 1961, as *Hystrichosphaeridea*).

Distatodinium ellipticum (Cookson 1965) n. comb.

Pl. 9, figs 7–9

1965 *Hystrichosphaeridium ellipticum* Cookson: 87; pl. 11, figs 1–3, 3a.
1969 *Tanyosphaeridium ellipticum* (Cookson) Davey & Williams: 7.
1972 *Tanyosphaeridium ellipticum* (Cookson) Davey & Williams; Benedek: 35; pl. 9, figs 13–14; pl. 10, fig. 2.

Description. The cyst body has an elongate oval outline and a smooth or finely granular surface. The processes are variable in breadth, simple or branched, typically flattened and blade-like in cross-section, and distally and proximally expanded. Distally they are bifurcate or trifurcate with complex secondary and tertiary branchlets, the ramifications having a twig-like appearance. The number of processes varies from about 40 to about 60. They appear to be present over all zones of the cyst body, but frequently show a greater concentration towards the apex and antapex. The processes show some alignment into rings around the cyst body, and a definite alignment into rows parallel to its long axis. The straight or curved lines marking the divergence of the processes from the cyst body are also parallel to the long axis. Occasionally processes occur which are T-shaped in cross-section. Adjacent longitudinally aligned processes may be proximally united by membrane, particularly at the antapex. Archaeopyle apical.

Dimensions. Observed range: cyst body (without operculum) $40 \times 25\ \mu$ to $73 \times 48\ \mu$; processes, length up to 30 μ, breadth up to 7 μ. (n = 24).

Remarks. The flattened processes appear to be essentially solid, particularly in the proximal region. Occasionally the distal ramifications may be hollow (Cookson 1965 : 87 ; pl. 11, fig. 3a), and some specimens of *D. ellipticum* have been recorded here with a few very slender tubular processes. The flattening and alignment of the processes parallel to the long axis of the cyst body in *D. ellipticum* may indicate that the processes are basically sutural in position, and the occasional process which is T-shaped in cross-section is probably gonal in position. However, the processes cannot be attributed to reflected tabulation zones as readily as in *D. craterum* n. sp., and their occasional arrangement in arcuate complexes complicates the interpretation of process distribution in *D. ellipticum.*

Occurrence. Upper Eocene.

Previous Records. Upper Eocene of Victoria, Australia (Cookson 1965) ; Middle and Upper Oligocene of north Germany (Benedek 1972).

Distatodinium paradoxum (Brosius 1963) n. comb.

Pl. 9, fig. 6

1963 *Hystrichosphaeridium paradoxum* Brosius : 41 ; pl. 4, figs 1, 6 ; text-fig. 2 (nos 1a–c).
1969 *Tanyosphaeridium paradoxum* (Brosius) Gocht : 54 ; pl. 7, figs 5–8 ; text-fig. 39.
1969 ? *Oligosphaeridium paradoxum* (Brosius) Davey & Williams : 5.
1972 *Tanyosphaeridium paradoxum* (Brosius) Gocht ; Benedek : 35 ; pl. 9, fig. 12 ; pl. 10, fig. 6.

Description. The cyst body has an oval or elongate oval outline and a smooth or finely granular surface. The processes are typically slender, simple or branched, distally and proximally expanded, usually flattened and blade-like in cross-section, occasionally tubular. Distally they are bifurcate or trifurcate with some secondary and tertiary branchlets at the extremities. The number of processes is about 20 and their distribution is similar to that of *D. craterum* n. sp. In addition to the alignment of the processes into rings around the cyst body, there is also some alignment into rows parallel to the long axis of the cyst body. The straight or curved lines marking the divergence of the processes from the cyst body are also usually parallel to the long axis. Adjacent longitudinally aligned processes may be proximally united by membrane. Archaeopyle apical. One specimen (Pl. 9, fig. 6) shows partial detachment of the polar region. If this is interpreted as the apical zone, the operculum bears four processes, two of which are proximally united by membrane.

Dimensions. Observed range : cyst body, length (with operculum) 46 μ, length (without operculum) 36–52 μ, breadth 28–42 μ ; length of processes up to 24 μ. (n = 6).

Remarks. As has been suggested for *D. craterum* n. sp., the processes in *D. paradoxum* are possibly sutural in position. On this basis, and assuming the polar breakage represents archaeopyle formation, the illustrated specimen can be interpreted as having four apical plates, six precingular plates, and at least five postcingular plates.

Occurrence. Upper Eocene.

Previous Records. Middle Oligocene of north Germany (Gocht 1969, Benedek 1972); Upper Oligocene of north Germany (Brosius 1963, Benedek 1972).

Genus ***EOCLADOPYXIS*** Morgenroth 1966a

Eocladopyxis peniculatum Morgenroth 1966a

Pl. 8, fig. 8

1966a *Eocladopyxis peniculatum* Morgenroth: 7; pl. 3, figs 2–3.

Dimensions. Observed range: diameter of cyst body 28–50 μ; length of processes up to 11 μ. (n = 12).

Remarks. The majority of the specimens here recorded show partial separation of the plate areas. The figured specimen shows the loss of the apical zone in archaeopyle formation, and the separation of the plates on the dorsal surface, particularly the narrow, elongate cingular plates.

Occurrence. Lower and Middle Eocene.

Previous Record. Lower Eocene of north Germany (Morgenroth 1966a).

Genus ***GONYAULACYSTA*** Deflandre *ex* Norris & Sarjeant 1965, emend. Sarjeant 1969

Gonyaulacysta tenuitabulata (Gerlach) De Coninck 1968

Fig. 14; Pl. 8, fig. 9

1961 *Gonyaulax tenuitabulata* Gerlach: 159; pl. 25, figs 10–11; text-figs 1–3.
1968 *Gonyaulacysta tenuitabulata* (Gerlach) De Coninck: 23; pl. 5, figs 9–10, 13–16.

Dimensions. Observed range: overall 48 × 42 μ to 88 × 84 μ; length of apical horn up to 8 μ. (n = 14).

Remarks. *G. tenuitabulata* has a delicate appearance, and the plate boundaries are marked by low, simple thickenings of the periphragm, defining a tabulation of 4′, 6″, 6c, 6‴, 1p, 1p.v., 1⁗.

Occurrence. Lower, Middle and Upper Eocene.

Previous Records. Lower Eocene of Belgium (De Coninck 1968); Middle Oligocene and Middle Miocene of north Germany (Gerlach 1961).

Genus ***HOMOTRYBLIUM*** Davey & Williams 1966b

Homotryblium tenuispinosum Davey & Williams 1966b

Pl. 10, fig. 1

1966b *Homotryblium tenuispinosum* Davey & Williams: 101; pl. 4, fig. 11; pl. 12, figs 1, 5, 7; text-fig. 21.

Dimensions. Observed range: cyst body 32 × 30 μ to 60 × 48 μ; length of processes up to 38 μ. (n = 8).

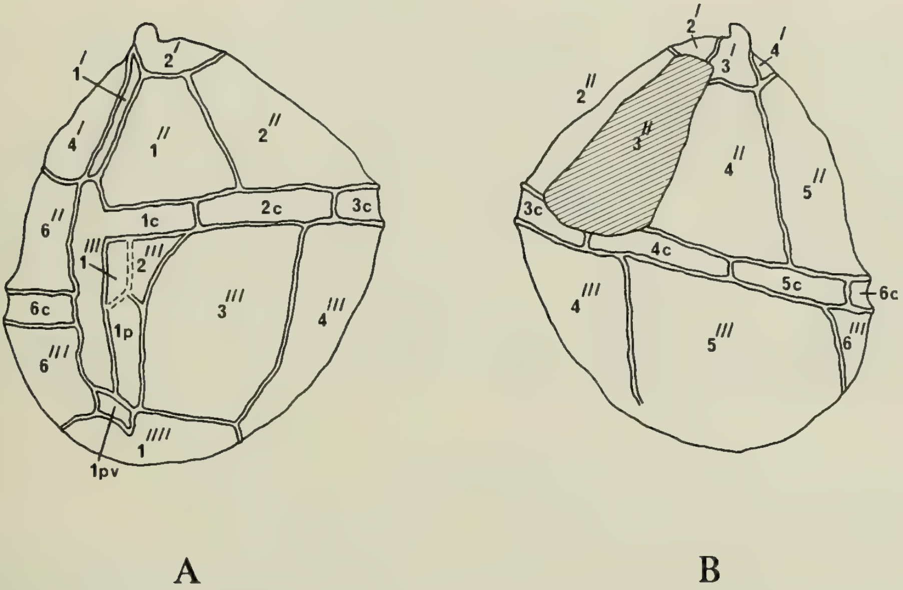


FIG. 14. *Gonyaulacysta tenuitabulata* (Gerlach) De Coninck 1968, reflected tabulation. A. Ventral view. B. Dorsal view, the precingular archaeopyle (3'') indicated by shading. V.57770 (2) ; W58.

OCCURRENCE. Lower, Middle and Upper Eocene.

PREVIOUS RECORDS. Lower Eocene of northern Spain (Caro 1973) and of the London Basin in southern England (Davey & Williams 1966b, Downie, Husain & Williams 1971*).

Homotryblium abbreviatum n. sp.

Pl. 10, figs 2–4

1968 *Hystrichosphaeridium tubiferum brevispinum* Davey & Williams ; De Coninck : 37 ; pl. 9, figs 24–25.

DERIVATION OF NAME. Latin, *abbreviatus*, shortened, with reference to the short processes.

DIAGNOSIS. Cyst body subspherical or spherical with a granular surface. Processes short, tubular and distally expanded ; distal margin denticulate, secate or aculeate. Length of processes not exceeding one-third of the mean diameter of the cyst body. Processes intratabular, one per reflected plate area. Reflected tabulation of the form 3–4', 6'', 6c, 5–6''', 0–1p, 1'''' ; archaeopyle epitractal.

HOLOTYPE. B.M.(N.H.) Palaeont. slide V.57782 (1). Sample AB11, bed 2g, Bracklesham Beds, Lower Eocene, Alum Bay, Isle of Wight, England.

Dimensions. Holotype: diameter of cyst body 48 μ; processes, length up to 12 μ, breadth up to 8 μ. Observed range: diameter of cyst body 34–48 μ; processes up to 14 μ, breadth up to 10 μ. (n = 11).

Remarks. The short processes may be slender or broad, and they are circular to subquadrate in section. The processes may show a proximal circle where they diverge from the cyst body. Up to five very slender processes have been observed on the sulcal zone. *H. abbreviatum* n. sp. differs from all described species of *Homotryblium* in having very short processes, the length of which does not exceed one-third of the mean diameter of the cyst body.

Occurrence. Lower, Middle and Upper Eocene.

Previous Record. Lower Eocene of Belgium (De Coninck 1968, as *Hystrichosphaeridium tubiferum brevispinum*).

Homotryblium oceanicum n. sp.

Pl. 10, figs 5–8

Derivation of Name. Latin, *oceanus*, the sea, ocean.

Diagnosis. Cyst body subspherical or spherical with a granular surface. Processes long, broad and cylindrical, and individually relatively constant in breadth, showing little distal expansion. Distal margin denticulate, secate or aculeate. Processes intratabular, one per reflected plate area. Reflected tabulation of the form 3′, 6″, 6c, 5‴, 1⁗; archaeopyle epitractal.

Holotype. B.M.(N.H.) Palaeont. slide V.57794 (1). Sample AB40, bed 19, Bracklesham Beds, Upper Eocene, Alum Bay, Isle of Wight, England.

Dimensions. Holotype: diameter of cyst body 49 μ; processes, length up to 28 μ, breadth up to 10 μ. Observed range: diameter of cyst body 36–50 μ; processes, length up to 30 μ, breadth up to 16 μ. (n = 12).

Remarks. The majority of the studied specimens are incomplete; no sulcal processes have been observed. In some specimens there is a proximal circle where the processes diverge from the cyst body. The distinctive long broad cylindrical processes, individually relatively constant in breadth, distinguish *H. oceanicum* from all described species of *Homotryblium.*

Occurrence. Middle and Upper Eocene.

Genus **HYSTRICHOKOLPOMA** Klumpp 1953 emend. Williams & Downie 1966a

Hystrichokolpoma eisenacki Williams & Downie 1966a

Pl. 10, fig. 9

1966a *Hystrichokolpoma eisenacki* Williams & Downie: 176; pl. 17, figs 1–3; text-fig. 46.

Dimensions. Observed range: diameter of cyst body 36–50 μ; large processes, length up to 28 μ, breadth up to 28 μ; antapical process, length up to 42 μ, breadth up to 20 μ; length of slender processes up to 20 μ. (n = 8).

Remarks. Williams & Downie (1966a) described *H. eisenacki* typically as having small tubules branching off from the large processes. In addition to the typical form of *H. eisenacki* recorded in this study, some specimens have been observed with both acuminate spines and tubules developed on the large processes.

Occurrence. Lower, Middle and Upper Eocene.

Previous Records. Lower Eocene of Belgium (De Coninck 1972*), of northern France (Gruas-Cavagnetto 1970b*), of north Germany (Gocht 1969) and of the Hampshire and London Basins in southern England (Williams & Downie 1966a); Middle and ? Upper Eocene of north Germany (Gocht 1969); Upper Eocene of East Prussia (Eisenack 1954, as *Hystrichokolpoma cinctum*); Eocene, undifferentiated, of Romania (Balteş 1969, doubtful attribution); Middle Oligocene of north Germany (Gocht 1969).

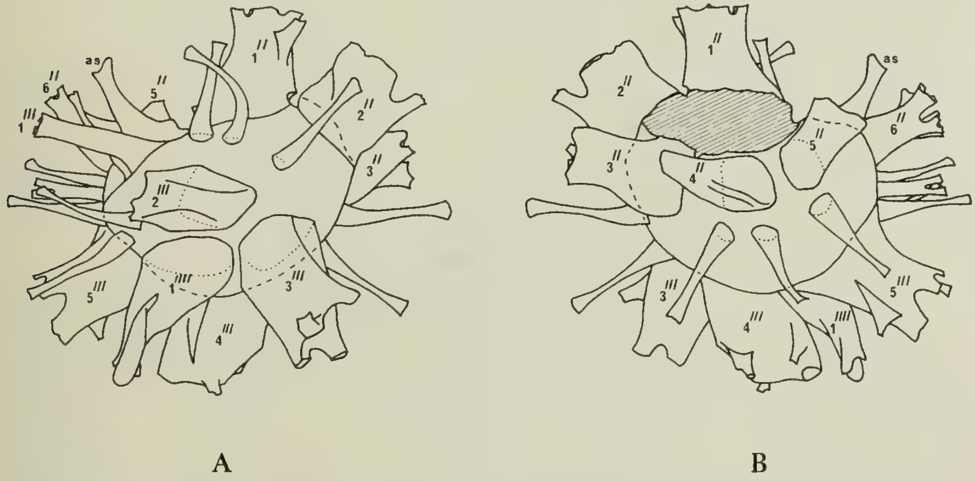


Fig. 15. *Hystrichokolpoma granulata* n. sp. Reflected tabulation of holotype. A. Ventral view. B. Dorsal view, the apical archaeopyle indicated by shading. V.57781 (6); AB11.

Hystrichokolpoma granulata n. sp.

Fig. 15; Pl. 10, figs 11–13

Derivation of Name. Latin, *granulum*, small grain, granule, with reference to the surface ornament.

Diagnosis. Cyst body subspherical with a granular surface. There are two types of granular intratabular processes. Large broad cylindrical processes, restricted to the pre- and postcingular and antapical zones, split distally into short open branches, and may exhibit distal tubules. Slender open processes, restricted to the cingular and sulcal zones, are distally expanded, simple or distally branched. Reflected tabulation 4′, 6″, 6c, 5‴, 1⁗; archaeopyle apical, tetratabular.

Holotype. B.M.(N.H.) Palaeont. slide V.57781 (6). Sample AB11, bed 2g, Bracklesham Beds, Lower Eocene, Alum Bay, Isle of Wight, England.

Dimensions. Holotype: cyst body (without operculum) 39 × 49 μ; large processes, length up to 20 μ, breadth up to 19 μ; antapical process, length 24 μ, breadth 16 μ; length of slender processes up to 24 μ. Observed range: diameter of cyst body (without operculum) 28–46 μ; large processes, length up to 20 μ, breadth up to 19 μ; antapical process, length up to 24 μ, breadth up to 16 μ; length of slender processes up to 24 μ. (n = 10).

Remarks. Unlike other species of *Hystrichokolpoma*, the individual plate areas are not clearly defined on the cyst body in *H. granulata* n. sp. On the cingular zone there are typically two, sometimes one process per plate. The antapical process is distinctive, tapering distally with tubules typically developed close to the distal margin. The anterior sulcal process (a.s.) is larger than the other sulcal processes. The form of the apical processes has not been determined. *H. granulata* is distinguished from other species of *Hystrichokolpoma* by its distinctive granular ornament, the overall form of the processes and the lack of well-defined plate areas on the cyst body.

Occurrence. Lower and Middle Eocene.

Hystrichokolpoma rigaudae Deflandre & Cookson 1955

Pl. 10, fig. 10

1955 *Hystrichokolpoma rigaudae* Deflandre & Cookson: 279; pl. 6, figs 6, 10; text-fig. 42.

Dimensions. Observed range: diameter of cyst body 32–42 μ; large processes, length up to 26 μ, breadth up to 9 μ; antapical process, length up to 26 μ, breadth up to 10 μ; length of slender processes up to 20 μ. (n = 10).

Remarks. The large processes in *H. rigaudae* are characterized by considerable distal expansion and the development of distal tubules.

Occurrence. Lower, Middle and Upper Eocene.

Previous Records. Palaeocene of Victoria, Australia (Cookson & Eisenack 1967b); Lower Eocene of Belgium (De Coninck 1965, 1967*, 1972*, Morgenroth 1966a), of northern France (Gruas-Cavagnetto 1968, 1970b), of north Germany (Morgenroth 1966a), of the Hampshire Basin (Williams & Downie 1966a) and of the London Basin in southern England (Williams & Downie 1966a, Graus-Cavagnetto 1970c*) and of Victoria (Deflandre & Cookson 1955); Middle Eocene of northern France (Gruas-Cavagnetto 1971*); ? Middle Eocene of Victoria (Deflandre & Cookson 1955): Upper Eocene of Victoria (Cookson & Eisenack 1965); Eocene, undifferentiated, of Victoria (Deflandre & Cookson 1955); Middle Oligocene of north Germany (Gerlach 1961, Benedek 1972); Upper Oligocene of north Germany (Gerlach 1961, Brosius 1963, Benedek 1972); Middle Miocene of north Germany (Maier 1959, Gerlach 1961); Miocene–Pliocene of Italy (Habib 1971*); Pleistocene of Israel (Rossignol 1962, 1964); Cenozoic, undifferentiated, of the eastern seaboard, U.S.A. (subsurface, offshore, Habib 1972).

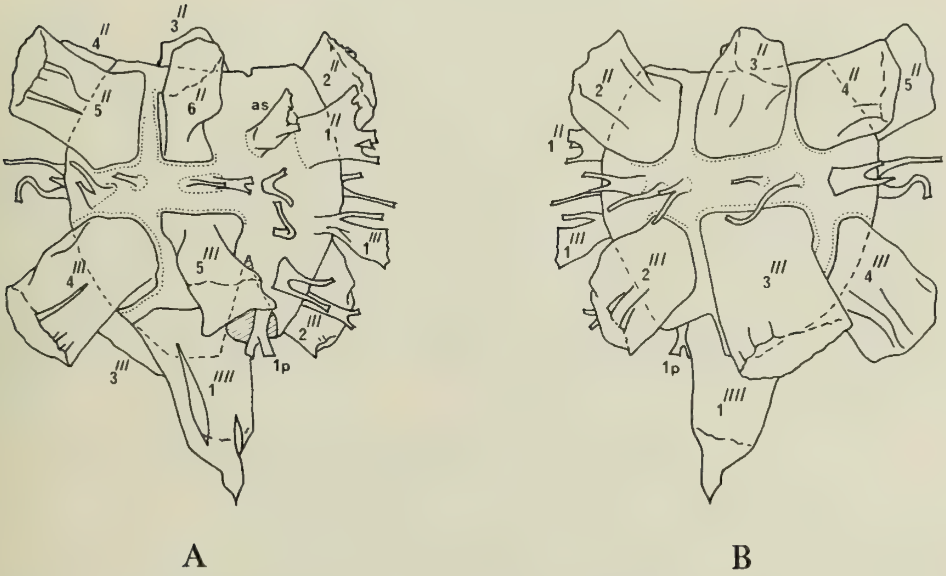


Fig. 16. *Hystrichokolpoma salacia* n. sp. Reflected tabulation of holotype. A. Ventral view. B. Dorsal view. V.57757 (6) ; W40.

Hystrichokolpoma salacia n. sp.

Fig. 16 ; Pl. 11, figs 1–3

Derivation of Name. Latin, *Salacia*, goddess of the sea.

Diagnosis. Cyst body subspherical with a smooth or finely granular surface. There are two types of intratabular processes. Large cylindrical processes, restricted to the pre- and postcingular and antapical zones, are subcircular or subquadrate in cross-section, distally closed, and the majority devoid of distal tubules. Processes 1'' and 1''' are reduced, may be branched and exhibit distal tubules. The slender processes, restricted to the cingular and sulcal zones, are simple or branched, and distally expanded and open. All processes have a finely striated surface. Reflected tabulation 4', 6'', 6c, 5''', 1p, 1'''' ; archaeopyle apical, tetratabular.

Holotype. B.M.(N.H.) Palaeont. slide V.57757 (6). Sample W40, bed 11, Bracklesham Beds, Middle Eocene, Whitecliff Bay, Isle of Wight, England.

Dimensions. Holotype : cyst body (without operculum) 46 × 44 μ ; large processes, length up to 23 μ, breadth up to 16 μ ; antapical process, length 26 μ, breadth 14 μ ; length of slender processes up to 10 μ. Observed range : diameter of cyst body (without operculum) 30–50 μ ; large processes, length up to 24 μ, breadth up to 18 μ ; antapical process, length up to 36 μ, breadth up to 18 μ ; length of slender processes up to 16 μ. (n = 20).

Remarks. The large closed cylindrical processes are devoid of distal tubules, but they frequently show longitudinal folds. The slender processes on the cingular zone are variable in form and number ; in most specimens there are two processes per cingular plate. The antapical process is considerably longer than the other large processes and differs in overall form ; it gradually tapers distally for about half to two-thirds of its length and then sharply to a restricted distal termination. The anterior sulcal process (a.s.) is larger than the other sulcal processes. The form of the apical processes has not been determined. The comparative simplicity of its large processes distinguishes *H. salacia* n. sp. from the majority of the described species of *Hystrichokolpoma*. *H. poculum* Maier 1959 also has simple large processes, but they were described by Maier (1959) as being cup-shaped and distally open.

Occurrence. Lower, Middle and Upper Eocene.

Previous Record. Possibly from the Eocene, undifferentiated, of Romania (Balteş 1969, as *Hystrichokolpoma eisenacki*).

Genus ***HYSTRICHOSPHAERIDIUM*** Deflandre 1937 emend. Davey & Williams 1966b

Hystrichosphaeridium tubiferum (Ehrenberg) Deflandre 1937 emend. Davey & Williams 1966b

Pl. 11, fig. 4

1838 *Xanthidium tubiferum* Ehrenberg : pl. 1, fig. 16.
1937 *Hystrichosphaeridium tubiferum* (Ehrenberg) Deflandre : 68.
1966b *Hystrichosphaeridium tubiferum* (Ehrenberg) Deflandre emend. Davey & Williams : 56 ; pl. 6, figs 1–2 ; pl. 8, fig. 5 ; pl. 10, fig. 2 ; text-fig. 13.

Dimensions. Observed range : cyst body $30 \times 35\ \mu$ to $48 \times 45\ \mu$; length of processes 12–$30\ \mu$. ($n = 6$).

Remarks. The specimens here attributed to *H. tubiferum* are similar to those recorded from the London Clay (Lower Eocene) of southern England by Davey & Williams (1966b). They exhibit slender tubular processes which show considerable distal expansion and a foliate distal margin. Occasionally some processes show the development of distal fenestration. Several records of *H. tubiferum* from the Lower Eocene and all illustrated records from younger Palaeogene and Neogene sediments in north-west Europe are probably referable to *Homotryblium* Davey & Williams 1966b ; the illustrated specimens exhibit either an epitractal archeopyle or the required process number and distribution for this genus, or both. These records are as follows : Lower Eocene of Belgium (De Coninck 1965 : 25 ; pl. 6, figs 1–3, 6–7) and of Belgium and north Germany (Morgenroth 1966a : 31 ; pl. 8, figs 7–8) ; Upper Eocene of north Germany (Agelopoulos 1967 : 37 ; pl. 11, fig. 2) ; Middle and Upper Oligocene of north Germany (Benedek 1972 : 30 ; pl. 9, fig. 5) ; Upper Oligocene of north Germany (Brosius 1963 : 38 ; pl. 8, fig. 4) ; Middle and Upper Oligocene and Middle Miocene of north Germany (Gerlach 1961 : 184 ; pl. 28, fig. 2). Gruas-Cavagnetto (1970a) recorded *H. tubiferum* in large numbers from the Upper Eocene of the Hampshire Basin in southern England. The material is not illustrated, but examination of equivalent horizons in this area indicates that the species occurring in large numbers is *Homotryblium tenuispinosum* Davey & Williams 1966b.

Occurrence. Lower Eocene.

Previous Records. Cretaceous, Albian and younger – see Davey & Verdier (1971); Lower Palaeocene (Danian) of California, U.S.A. (Drugg 1967); Palaeocene to Lower Eocene of New Zealand (Wilson 1968*); Lower Eocene of Belgium (De Coninck 1967*, 1968, 1972*, Gruas-Cavagnetto 1968), of northern France (Gruas-Cavagnetto 1970b) and of the Hampshire and London Basins in southern England (Davey & Williams 1966b, Downie, Husain & Williams 1971*); Middle Eocene of northern France (Gruas-Cavagnetto 1971*); Eocene, undifferentiated, of Argentina (Archangelsky 1969, doubtful attribution); Lower Tertiary, undifferentiated, of Antarctica, in erratics (McIntyre & Wilson 1966*, Wilson 1967a) and of Tierra del Fuego, Argentina (Baldis 1966); ? Tertiary of Victoria, Australia (Cookson 1953, doubtful attribution); Pleistocene of Israel (Rossignol 1964, presumably as reworking).

Hystrichosphaeridium asterium n. sp.

Pl. 11, figs 7–10

1972 *Hystrichosphaeridium pseudorecurvatum* Morgenroth; Benedek: 29; pl. 9, fig. 10.

Derivation of Name. Greek ἀστέριος, starry, with reference to the distinctive distal termination of the processes.

Diagnosis. Cyst body has a subcircular or rounded polygonal outline and a smooth surface. Processes about 20, tubular and usually slender and fairly constant in breadth. Each process is surmounted by a wide distal platform with usually 10 to 15 marginal aculei. Archaeopyle apical.

Holotype. B.M.(N.H.) Palaeont. slide V.57772 (3). Sample W58, bed 19c, Bracklesham Beds, Upper Eocene, Whitecliff Bay, Isle of Wight, England.

Dimensions. Holotype: cyst body (without operculum) 27 × 32 μ; length of processes up to 13 μ. Observed range: cyst body (without operculum) 22 × 22 μ to 30 × 34 μ; length of processes up to 20 μ. (n = 4).

Remarks. None of the observed specimens is complete. The number of processes (about 20) indicates that there is one process per plate, reflecting the tabulation of the genus. The processes are occasionally expanded proximally – in one specimen (Pl. 11, fig. 9) one process shows considerable proximal expansion. The distal platforms which surmount each process are typically recurved, sometimes flat or slightly concave. Some processes show a reduction of the distal platform; these are similar to those of *H. pseudorecurvatum* Morgenroth 1966a. Apart from the occasional presence of such processes, the small size of *H. asterium* and the distinctive form of the distal portion of its processes distinguish this species from all other described species of *Hystrichosphaeridium*.

Occurrence. Upper Eocene.

Previous Record. Middle Oligocene of north Germany (Benedek 1972, as *H. pseudorecurvatum*).

Hystrichosphaeridium patulum Davey & Williams 1966b

Pl. 11, fig. 5

1966b *Hystrichosphaeridium patulum* Davey & Williams : 60 ; pl. 10, fig. 5.

Dimensions. Observed range : diameter of cyst body 12–20 μ ; length of processes 4–8 μ. (n = 7).

Occurrence. Lower, Middle and Upper Eocene.

Previous Records. Lower Eocene of Belgium (De Coninck 1968) and of the Hampshire and London Basins in southern England (Davey & Williams 1966b).

Hystrichosphaeridium pseudorecurvatum Morgenroth 1966a

Pl. 11, fig. 6

1966a *Hystrichosphaeridium pseudorecurvatum* Morgenroth : 30 ; pl. 8, figs 5–6.

Dimensions. Observed range : diameter of cyst body 21–33 μ ; length of processes 8–20 μ. (n = 10).

Remarks. Morgenroth (1966a) noted up to 35 processes in some specimens of *H. pseudorecurvatum*, indicating that there may be more than one process on some plates. A variation in process number was also noted in this study, some specimens having up to 60 processes.

Occurrence. Lower, Middle and Upper Eocene.

Previous Records. Lower Eocene of Belgium (Morgenroth 1966a, Gruas-Cavagnetto 1968, De Coninck 1968), of northern France (Gruas-Cavagnetto 1970b*), of north Germany (Morgenroth 1966a) and of the Hampshire and London Basins in southern England (Davey & Williams 1966b, as *H. sheppeyense*) ; Middle Eocene of northern France (Gruas-Cavagnetto 1971*) ; Upper Eocene of Belgium (Rozen 1965, as *H. recurvatum*).

Genus ***LANTERNOSPHAERIDIUM*** Morgenroth 1966a

Lanternosphaeridium lanosum Morgenroth 1966a

Pl. 12, fig. 1

1966a *Lanternosphaeridium lanosum* Morgenroth : 38 ; pl. 10, figs 10–11.

Dimensions. Observed range : cyst body 60 × 44 μ to 68 × 50 μ ; height of membrane up to 22 μ ; length of apical horn up to 20 μ. (n = 2).

Remarks. A strong simple horn is frequently developed at the apical pole. The dense fibrous membrane present over the cyst body does not show any organization into discrete processes.

Occurrence. Lower Eocene.

Previous Records. Lower Eocene of Belgium and north Germany (Morgenroth 1966a).

Lanternosphaeridium axiale (Eisenack) Morgenroth 1966a

Pl. 12, fig. 2

1965 *Cordosphaeridium axiale* Eisenack : 150 ; pl. 15, figs 1–4.
1966a *Lanternosphaeridium axialis* (Eisenack) Morgenroth : 38 ; pl. 6, figs 4–5.
1969 *Lanternosphaeridium axiale* (Eisenack) Morgenroth ; Gocht : 48 ; pl. 2, figs 7–8 ; text-fig. 34.

Dimensions. Observed range : cyst body $48 \times 42\ \mu$ to $81 \times 63\ \mu$; length of processes up to $19\ \mu$; length of apical horn up to $21\ \mu$. $(n = 8)$.

Remarks. The numerous slender, fibrous, intratabular processes are distally expanded, usually simple, but sometimes branched.

Occurrence. Lower, Middle and Upper Eocene.

Previous Records. Lower Eocene of Belgium (Morgenroth 1966a) and of north Germany (Morgenroth 1966a, Gocht 1969) ; Middle Eocene of north Germany (Gocht 1969) ; Upper Eocene of north Germany (Eisenack 1965) ; ? Upper Eocene of north Germany (Gocht 1969) ; Middle Oligocene of north Germany (Gocht 1969).

Lanternosphaeridium radiatum Morgenroth 1966a

Pl. 12, fig. 3

1966a *Lanternosphaeridium radiatum* Morgenroth : 37 ; pl. 10, figs 7–9.

Dimensions. Observed range : cyst body $52 \times 40\ \mu$ to $81 \times 69\ \mu$; length of processes up to $24\ \mu$; length of apical horn up to $48\ \mu$. $(n = 17)$.

Remarks. The numerous fibrous intratabular processes are simple or branched, variable in breadth, frequently distally expanded, and usually proximally united by fibrous membrane.

Occurrence. Lower, Middle and Upper Eocene.

Previous Records. Lower Eocene of Belgium and north Germany (Morgenroth 1966a).

Lanternosphaeridium vectense n. sp.

Pl. 12, figs 4–6

Derivation of Name. From *Vectis*, the Roman name for the Isle of Wight, the type locality for this species.

Diagnosis. Cyst body subspherical, longer than broad, with a strongly fibro-reticulate surface. Usually between 50 and 60 fibrous, intratabular processes which are strong, variable in breadth, and simple or branched. They are proximally and distally expanded, and their length is less than half the mean diameter of the cyst body. The distal margins are ragged or aculeate. Apical horn strong and laterally expanded into usually three short branches. Archaeopyle precingular, formed by displacement of plate 3''.

HOLOTYPE. B.M.(N.H.) Palaeont. slide V.57797 (2). Sample AB40, bed 19, Bracklesham Beds, Upper Eocene, Alum Bay, Isle of Wight, England.

DIMENSIONS. Holotype: cyst body $95 \times 83\ \mu$; length of processes up to $31\ \mu$; length of apical horn $24\ \mu$. Observed range: cyst body $66 \times 55\ \mu$ to $95 \times 83\ \mu$; length of processes up to $31\ \mu$; length of apical horn up to $24\ \mu$. ($n = 18$).

REMARKS. The apical horn is typically shorter than the longest processes. The processes show considerable variation in breadth, very slender ones frequently reflecting the sulcal zone. *L. vectense* n. sp. is distinguished from *L. axiale* (Eisenack) Morgenroth 1966a by usually having a larger cyst body with a strongly fibro-reticulate surface and stronger, frequently broader processes, and from *L. radiatum* Morgenroth 1966a by having stronger discrete processes which are not proximally united by fibrous membrane.

OCCURRENCE. Middle and Upper Eocene.

Genus ***LEPTODINIUM*** Klement 1960, emend. Wall 1967, emend. Sarjeant 1969

Leptodinium membranigerum Gerlach 1961

Pl. 8, fig. 11

1961 *Leptodinium membranigerum* Gerlach: 162; pl. 26, figs 1–4, 7; text-figs 4–5.

DIMENSIONS. Observed range: cyst body $48 \times 46\ \mu$ to $66 \times 68\ \mu$; height of crests up to $8\ \mu$. ($n = 7$).

REMARKS. The cyst body has a finely punctate or finely granular surface. The sutural crests are unornamented or finely granular with a smooth or slightly serrated distal margin. A very low apical prominence is sometimes developed by separation of the periphragm and endophragm.

OCCURRENCE. Lower, Middle and Upper Eocene.

PREVIOUS RECORDS. Upper Oligocene and ? Middle Miocene of north Germany (Gerlach 1961).

Genus ***LINGULODINIUM*** Wall 1967

Lingulodinium machaerophorum (Deflandre & Cookson) Wall 1967

Pl. 8, fig. 10

1955 *Hystrichosphaeridium machaerophorum* Deflandre & Cookson: 274; pl. 9, figs 4, 8.
1967 *Lingulodinium machaerophorum* (Deflandre & Cookson) Wall: 109; pl. 15, figs 16–17; text-fig. 6.

DIMENSIONS. Observed range: diameter of cyst body $39–54\ \mu$; length of processes up to $22\ \mu$. ($n = 8$).

Occurrence. Lower, Middle and Upper Eocene.

Previous Records. Lower Palaeocene (Danian) of California (Drugg 1967, doubtful attribution); Lower Eocene of Belgium (De Coninck 1968), of northern France (Gruas-Cavagnetto 1968) and of north Germany (Morgenroth 1966a); Middle Eocene of northern France (Gruas-Cavagnetto 1971*); Upper Eocene of the Hampshire Basin in southern England (Gruas-Cavagnetto 1970a*); Middle Oligocene of north Germany (Gerlach 1961, Benedek 1972); Upper Oligocene of north Germany (Brosius 1963, Benedek 1972); ? Upper Oligocene of north Germany (Gerlach 1961); Middle Miocene of north Germany (Maier 1959, Gerlach 1961) and of Victoria, Australia (Deflandre & Cookson 1955); Miocene–Pliocene of Italy (Habib 1971); Pleistocene of the Caribbean Sea (Wall 1967), of Israel (Rossignol 1962, as *Hystrichosphaeridium ashdodense*; 1964) and of Norfolk, England (subsurface, Wall & Dale 1968b*). *L. machaerophorum* has also been recorded from Recent sediments, e.g. Wall & Dale (1967).

Genus ***LITOSPHAERIDIUM*** Davey & Williams 1966b

Litosphaeridium ? inversibuccinum Davey & Williams 1966b

Pl. 13, figs 1–5

1966b ? *Litosphaeridium inversibuccinum* Davey & Williams: 82; pl. 12, fig. 3.

Description. The forms here assigned to *L.? inversibuccinum* invariably exhibit a polygonal apical archaeopyle, and 12 or 14 processes arranged in two rings which are presumed to reflect the pre- and postcingular zones. No processes have been observed at the antapex. Distally the processes are tubular with an expanded denticulate or aculeate margin; proximally they are hollow and considerably expanded, and laterally adjacent processes merge into each other. Six or eight processes have been recorded on the precingular zone, and six on the postcingular zone. The generic assignment of this species remains uncertain.

Dimensions. Observed range: diameter of cyst body 12–18 μ; length of processes up to 12 μ. (n = 5).

Occurrence. Lower, Middle and Upper Eocene.

Previous Records. Lower Eocene of Belgium (De Coninck 1968) and of the Hampshire and London Basins in southern England (Davey & Williams 1966b, Downie, Husain & Williams 1971*).

Genus ***MEMBRANILARNACIA*** Eisenack 1963a emend. Williams & Downie 1966c

Membranilarnacia ursulae (Morgenroth) De Coninck 1968

Pl. 12, fig. 7

1966a	*Cannosphaeropsis ursulae* Morgenroth: 20; pl. 3, figs 11–12.
1966c	*Membranilarnacia reticulata* Williams & Downie: 220; pl. 24, figs 4, 6; text-fig. 59.
1967	*Membranilarnacia diktyophora* Agelopoulos: 49; pl. 12, figs 3–4, 6.
1968	*Membranilarnacia ursulae* (Morgenroth) De Coninck: 43; pl. 13, figs 4–6.

DIMENSIONS. Observed range: diameter of cyst body 36–53 μ; length of processes up to 32 μ. (n = 3).

REMARKS. Williams & Downie (1966c) recognized two variants of this distinctive species (described as *M. reticulata* Williams & Downie 1966c) in the London Clay (Lower Eocene) of southern England. One has processes on the cingular zone, the other is devoid of processes on this zone, the latter being the more common variant. The specimens here attributed to *M. ursulae* are referable to the more common of the two variants.

OCCURRENCE. Lower and Middle Eocene.

PREVIOUS RECORDS. Lower Eocene of Belgium (Morgenroth 1966a, De Coninck 1968, 1972*), of north Germany (Morgenroth 1966a), of the Hampshire Basin (Williams & Downie 1966c, as *M. reticulata*; Downie, Husain & Williams 1971*, Eaton 1971a) and the London Basin in southern England (Williams & Downie 1966c, as *M. reticulata*; Downie, Husain & Williams 1971*); Middle Eocene of north Germany (Gocht 1969) and of the Hampshire Basin (Eaton 1971a); Upper Eocene of north Germany (O. Wetzel 1935, as *Membranilarnax* sp. indet.; Eisenack 1954, as *Membranilarnax* sp. indet.; Agelopoulos 1967, as *Membranilarnacia diktyophora*).

Genus ***OPERCULODINIUM*** Wall 1967

Operculodinium centrocarpum (Deflandre & Cookson) Wall 1967

Pl. 15, figs 1–2

1955 *Hystrichosphaeridium centrocarpum* Deflandre & Cookson: 272; pl. 8, figs 3–4.
1967 *Operculodinium centrocarpum* (Deflandre & Cookson) Wall: 111; pl. 16, figs 1–2, 5.

DIMENSIONS. Observed range: diameter of cyst body 28–75 μ; length of processes up to 31 μ. (n = 22).

OCCURRENCE. Lower, Middle and Upper Eocene.

PREVIOUS RECORDS. Upper Cretaceous (Senonian) of Natal, South Africa (Davey 1969a); Lower Palaeocene (Danian) of California, U.S.A. (Drugg 1967); Lower Eocene of Belgium (Morgenroth 1966a, De Coninck 1968, Gruas-Cavagnetto 1968) and of north Germany (Morgenroth 1966a); Middle Eocene of northern France (Gruas-Cavagnetto 1971*); Middle and Upper Eocene of the Hampshire Basin in southern England (Gruas-Cavagnetto 1970a*); Upper Eocene of north Germany (Agelopoulos 1967, doubtful attribution); Middle Oligocene of north Germany (Maier 1959, Gerlach 1961); Upper Oligocene of north Germany (Maier 1959, Gerlach 1961, Brosius 1963); Oligocene, undifferentiated, of Victoria, Australia (Cookson 1953, as *Hystrichosphaeridium* sp. b); Middle Miocene of north Germany (Maier 1959, Gerlach 1961) and of Victoria (Cookson, 1953, as *Hystrichosphaeridium* sp. a; Deflandre & Cookson 1955); Upper Miocene of north Germany (Maier 1959); Miocene–Pliocene of Italy (Habib 1971); Pleistocene of the Caribbean Sea (Wall 1967) and of Norfolk, England (subsurface, Wall & Dale 1968b); Cenozoic, undifferentiated, of the eastern seaboard, U.S.A. (subsurface, offshore, Habib 1972). *O. centrocarpum* has also been recorded from Recent sediments, e.g. Wall & Dale (1967).

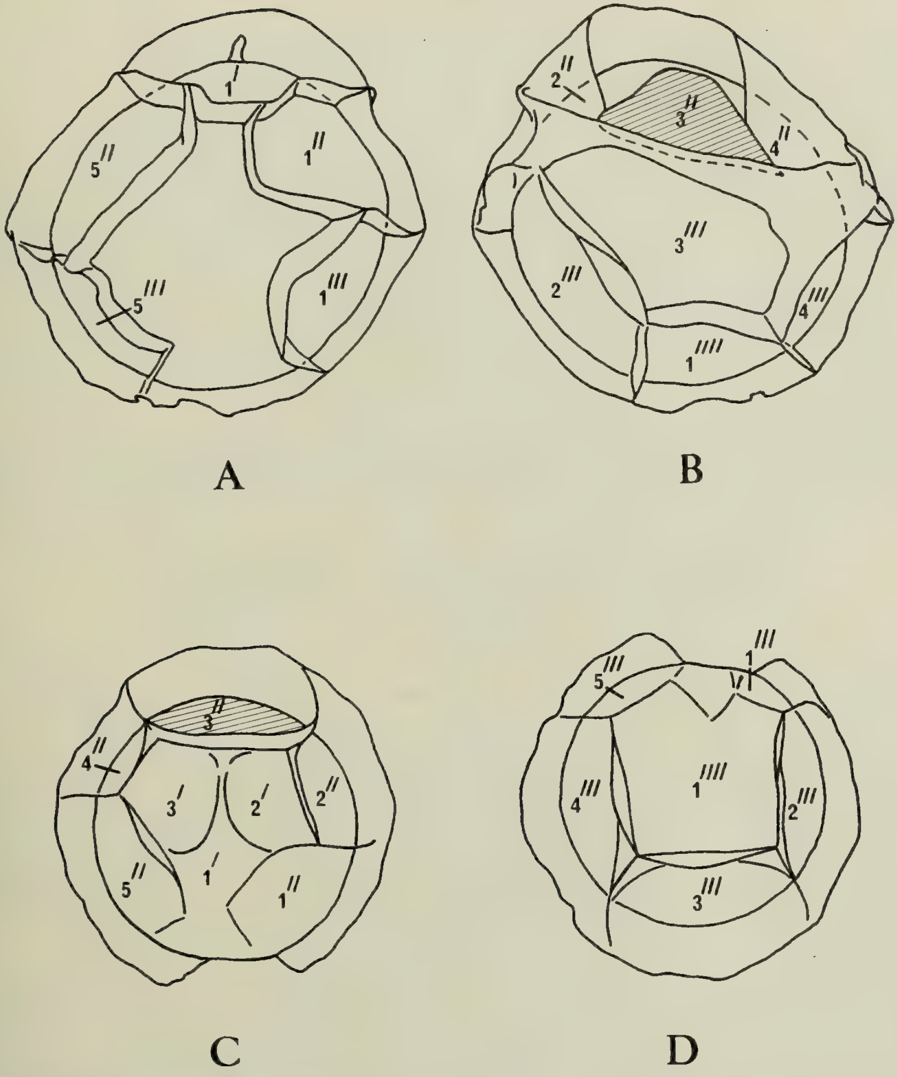


FIG. 17. *Pentadinium laticinctum* Gerlach 1961. A, B. Ventral and dorsal views respectively. V.57750 (4) ; W32. C, D. Apical and antapical views respectively. V.57752 ; W37. The precingular archaeopyle (3″) is indicated by shading.

Genus ***PENTADINIUM*** Gerlach 1961

Pentadinium laticinctum Gerlach 1961

Fig. 17 ; Pl. 13, figs 6–11

1961 *Pentadinium laticinctum* Gerlach : 165 ; pl. 26, figs 5–6 ; text-figs 6–7.

DESCRIPTION. The overall cyst shape is rounded polygonal to subspherical.

Endophragm spherical or subspherical, thick-walled with an irregularly granular surface; surrounding periphragm thin, its surface smooth or granular. Plate boundaries marked by linear thickenings of the periphragm, sutural crests with undulating or irregular distal margins or linear folds in the periphragm. Reflected tabulation 1–3′, 5″, 5‴, 1⁗. The apical zone is usually occupied by a single large polygonal plate, although occasionally three plates are distinguishable (Fig. 17C). A short apical projection may be present at the apical pole (Fig. 17A). The precingular and postcingular zones are separated by a single sutural crest, which is slightly helicoid and is interrupted by the sulcal zone. The sulcal zone is broadest where its boundaries meet the cingular crest (Fig. 17A). The archaeopyle is precingular, formed by the displacement of plate 3″.

Dimensions. Observed range: overall 56 × 56 μ to 74 × 78 μ; endophragm 48 × 48 μ to 62 × 62 μ. (n = 8).

Occurrence. Lower, Middle and Upper Eocene.

Previous Records. Middle and Upper Oligocene of north Germany (Gerlach 1961, Benedek 1972); Middle Miocene of north Germany (Gerlach 1961).

Genus ***POLYSPHAERIDIUM*** Davey & Williams 1966b

Polysphaeridium subtile Davey & Williams 1966b

Pl. 14, figs 1–2

1966b *Polysphaeridium subtile* Davey & Williams: 92; pl. 11, fig. 1.

Dimensions. Observed range: diameter of cyst body 36–50 μ; length of processes up to 15 μ. (n = 12).

Remarks. Specimens here assigned to *P. subtile* frequently exhibit an epitractal archaeopyle. In the generic diagnosis of *Polysphaeridium* the archaeopyle is described as being apical with an angular margin, when present (Davey & Williams 1966b: 92). In the original diagnosis and description of *P. subtile* (the type species of *Polysphaeridium*) no mention is made of the position and form of the archaeopyle. The holotype (Davey & Williams 1966b: pl. 11, fig. 1) appears to show a breakage splitting the cyst body into two halves, suggesting an epitractal archaeopyle. On the basis of this evidence the diagnoses of *Polysphaeridium* and *P. subtile* should be emended to include reference to the epitractal archaeopyle. This would render *Hemicystodinium* Wall 1967 a junior synonym of *Polysphaeridium* since the former genus is also characterized by an epitractal archaeopyle and numerous processes. All the other species at present assigned to *Polysphaeridium* on the basis of their having an apical archaeopyle would then require assignment to a new genus with one of these species as the genotype. These taxonomic changes have not been effected here since none of the other species attributed to *Polysphaeridium* by Davey & Williams (1966b) was recorded in this study.

Occurrence. Lower, Middle and Upper Eocene.

Previous Records. Palaeocene and Lower Eocene of northern Spain (Caro 1973); Lower Eocene of the London Basin in southern England (Davey & Williams 1966b, Gruas-Cavagnetto 1970c*).

Genus ***SAMLANDIA*** Eisenack 1954

Samlandia chlamydophora Eisenack 1954

Pl. 15, fig. 3

1954 *Samlandia chlamydophora* Eisenack : 76 ; pl. 11, figs 12–15.

DIMENSIONS. Observed range : overall 74 × 50 μ to 110 × 80 μ ; endophragm 54 × 44 μ to 80 × 78 μ ; height of pillars up to 10 μ ; length of apical horn up to 20 μ. (n = 15).

REMARKS. The periphragm forms relatively thick, striated pillars or ridges whose distribution over the cyst body results in the formation of a series of circular or polygonal fields. The pillars are distally united by a thin membrane. A simple precingular archaeopyle is frequently recognizable.

OCCURRENCE. Lower, Middle and Upper Eocene.

PREVIOUS RECORDS. Lower Eocene of Belgium (Morgenroth 1966a, De Coninck 1972*) and of north Germany (Morgenroth 1966a) ; Upper Eocene of north Germany (Agelopoulos 1967) and of East Prussia (Eisenack 1954) ; Middle Oligocene of north Germany (Benedek 1972).

Genus ***SPINIFERITES*** Mantell 1850 emend. Sarjeant 1970

Spiniferites ramosus (Ehrenberg) Mantell 1854

Pl. 14, figs 3–7

1838 *Xanthidium ramosum* Ehrenberg : pl. 1, figs 1–2, 5.
1854 *Spiniferites ramosus* (Ehrenberg) Mantell : fig. 77, nos 4, 6.
1932 *Hystrichosphaera ramosa* (Ehrenberg) O. Wetzel : 144.

REMARKS. Specimens here attributed to *Spiniferites ramosus* exhibit a considerable range of variation in process length, development of membrane between the processes, and surface ornament. This has been expressed by Davey & Williams (1966a) in their description of several varieties of *S. ramosus* (as *Hystrichosphaera ramosa*), of which the following are here recognized.

Spiniferites ramosus var. *ramosus* Davey & Williams 1966a	Pl. 14, fig. 3
Spiniferites ramosus var. *granomembranaceus* Davey & Williams 1966a	Pl. 14, fig. 5
Spiniferites ramosus var. *granosus* Davey & Williams 1966a	Pl. 14, fig. 4
Spiniferites ramosus var. *membranaceus* (Rossignol) Davey & Williams 1966a	Pl. 14, fig. 7
Spiniferites ramosus var. *multibrevis* Davey & Williams 1966a	Pl. 14, fig. 6

OCCURRENCE. All forms occur in the Lower, Middle and Upper Eocene.

PREVIOUS RECORDS. (*S. ramosus* s.l.) Lower Cretaceous (Valanginian) to Recent, world wide in distribution.

Spiniferites cingulatus (O. Wetzel) Sarjeant 1970

Pl. 14, fig. 11

1933 *Cymatiosphaera cingulata* O. Wetzel : 28 ; pl. 4, fig. 10.
1954 *Hystrichosphaera cingulata* (O. Wetzel) Deflandre : 258.
1970 *Spiniferites cingulatus* (O. Wetzel) Sarjeant : 76.

Dimensions. Observed range: diameter of cyst body 46–56 μ; height of crests up to 16 μ. (n = 4).

Occurrence. Lower and Middle Eocene.

Previous Records. Cretaceous (Albian) to Pleistocene – see Davey & Verdier (1971).

Spiniferites cornutus (Gerlach) Sarjeant 1970

Pl. 14, fig. 10

1961 *Hystrichosphaera cornuta* Gerlach: 180; pl. 27, figs 10–12.
1970 *Spiniferites cornutus* (Gerlach) Sarjeant: 76.

Dimensions. Observed range: cyst body 52 × 40 μ to 56 × 56 μ; length of processes up to 13 μ; length of apical horn up to 24 μ. (n = 3).

Occurrence. Upper Eocene.

Previous Records. Lower Eocene of Belgium (De Coninck 1968) and of the Hampshire and London Basins in southern England (Davey & Williams 1966a); Upper Eocene of north Germany (Agelopoulos 1967); Middle Oligocene of north Germany (Gerlach 1961, Benedek 1972); Upper Oligocene of north Germany (Benedek 1972); Middle Miocene of north Germany (Gerlach 1961).

Spiniferites monilis (Davey & Williams) Sarjeant 1970 emend. herein

Pl. 14, figs 8–9

1966a *Hystrichosphaera monilis* Davey & Williams: 45; pl. 5, fig. 2.
1970 *Spiniferites monilis* (Davey & Williams) Sarjeant: 76.

Emended Diagnosis. A species of *Spiniferites* with a spherical or subspherical cyst body and a smooth or finely granular surface. Processes short, simple or branched; distally simple or furcate. Furcations taeniate, simple or branched, their distal margin entire, aculeate or secate.

Dimensions. Observed range: diameter of cyst body 21–44 μ; length of processes up to 12 μ. (n = 14).

Remarks. Davey & Williams (1966a) considered the presence of granules concentrated along the plate boundaries to be a characteristic feature of *S. monilis*. Examination of the holotype and morphologically similar forms from the Bracklesham Beds indicates that the 'sutural ornamentation' in fact consists of small depressions or pits, the development of which is a secondary effect probably due to the presence of pyrite (Neves & Sullivan 1964). As well as being concentrated along the plate boundaries, the pits may occupy large areas on the surface of the cyst body, while in other specimens there is no pit development. This secondary 'ornamentation' effect has also been observed in other taxa, and does not constitute a means of taxonomic distinction. However, *S. monilis* is still a morphologically distinct and valid species.

Occurrence. Lower, Middle and Upper Eocene.

Previous Records. Lower Eocene of the Hampshire and London Basins in southern England (Davey & Williams 1966a).

Spiniferites pseudofurcatus (Klumpp) Sarjeant 1970

Pl. 14, figs 12–13

1953 *Hystrichokibotium pseudofurcatum* Klumpp : 388 ; pl. 16, figs 12–14.
1960 *Hystrichosphaera tertiaria* Eisenack & Gocht : 515 ; text-fig. 4.
1966a *Hystrichosphaera buccina* Davey & Williams : 42 ; pl. 4, fig. 1, text-figs 10–11.
1969 *Hystrichosphaera pseudofurcata* (Klumpp) Gocht : 32 ; pl. 4, figs 12–13 ; text-fig. 22.
1970 *Spiniferites pseudofurcatus* (Klumpp) Sarjeant : 76.
1970 *Spiniferites buccinus* (Davey & Williams) Sarjeant : 75.

Dimensions. Observed range : diameter of cyst body 45–61 μ ; length of processes up to 30 μ. (n = 7).

Remarks. The taxonomic problems concerning this species have been discussed by Morgenroth (1966a), Gocht (1969) and Sarjeant (1970). Wall (1967 : 103) considered the tabulation pattern of *Hystrichosphaera tertiaria* Eisenack & Gocht 1960 (a junior synonym of *S. pseudofurcatus*) to be typically 'gonyaulacid', and not as originally described by Eisenack & Gocht 1960. This removes the only significant difference between this species and *Spiniferites buccinus* (Davey & Williams) Sarjeant 1970, and the latter species is also considered to be a junior synonym of *S. pseudofurcatus*.

Occurrence. Lower, Middle and Upper Eocene.

Previous Records. Lower Eocene of Belgium (Morgenroth 1966a, as *Hystrichosphaera incerta* ; De Coninck 1965, 1967*, as *Hystrichosphaera tertiaria*, doubtful attributions ; De Coninck 1968, as *Hystrichosphaera* cf. *tertiaria*), of northern France (Gruas-Cavagnetto 1970b, as *Hystrichosphaera buccina*), of north Germany (Morgenroth 1966a, as *Hystrichosphaera incerta* ; Gocht 1969) and of the Hampshire and London Basins in southern England (Davey & Williams 1966a, Downie, Husain & Williams 1971, both as *Hystrichosphaera buccina*) ; Middle Eocene of north Germany (Agelopoulos 1967, as *Hystrichosphaera furcata* and *H. tertiaria* ; Gocht 1969) ; Upper Eocene of north Germany (Klumpp 1953, also as *Areoligera incerta* and *Hystrichosphaera furcata* ; Agelopoulos 1967, as *Hystrichosphaera furcata* and *H. tertiaria*), of East Prussia (Eisenack 1954, as *Hystrichosphaera* cf. *furcata* ; Eisenack & Gocht 1960, as *Hystrichosphaera tertiaria*) ; ? Upper Eocene of north Germany (Gocht 1969) ; Eocene, undifferentiated, of Argentina (Archangelsky 1968, 1969*, as *Hystrichosphaera buccina*, doubtful attributions) ; Middle Oligocene of north Germany (Maier 1959, as *Areoligera* cf. *incerta* ; Gerlach 1961, also as *Hystrichosphaera furcata* ; Benedek 1972) ; questionably from the Middle Oligocene of north Germany (Gocht 1969) ; Upper Oligocene of north Germany (Gerlach 1961, also as *Hystrichosphaera furcata* ; Brosius 1963, as *Hystrichosphaera tertiaria* ; Benedek 1972) ; Middle Miocene of north Germany (Maier 1959, as *Areoligera* cf. *incerta* ; Gerlach 1961, also as *Hystrichosphaera furcata*) ; Miocene–Pliocene of Italy (Habib 1971, as *Spiniferites* sp.).

Genus ***THALASSIPHORA*** Eisenack & Gocht 1960

Eisenack & Gocht (1960) described *Thalassiphora* as consisting of a spherical or ellipsoidal central body (endophragm) surrounded by a bowl-shaped membrane (periphragm), implying that a large opening is present on the ventral surface of the periphragm in the type species, *Thalassiphora pelagica* (Eisenack) Eisenack & Gocht 1960. The majority of the specimens here assigned to *T. pelagica* also exhibit this large opening on the ventral surface, but in a few forms the small central body appears to be completely surrounded by periphragm on the ventral and dorsal surfaces.

Gocht (1968: pl. 25; 1969: text-fig. 46) illustrated his interpretation of the development of *T. pelagica*, based on material from the Eocene and Middle Oligocene of north Germany. He suggested that in its initial stages *T. pelagica* consists of a thick-walled central body (endophragm) closely surrounded by the periphragm in which linear folds and thickenings define a reflected tabulation of 1′, 1a, 5″, 4‴, 1⁗; Lf (Gocht 1968: pl. 25, figs 1–2; 1969: text-fig. 46a–b). At this stage the overall morphology is totally removed from that of the 'typical' *T. pelagica*. Through a series of intermediate stages the periphragm becomes ventrally concave and develops a ventral opening in the area of the longitudinal furrow (Lf), exposing the endophragm. The periphragm becomes well separated from the endophragm apart from the contact zone on the mid-dorsal surface, and the folds and thickenings which mark the plate boundaries become less clearly defined. The periphragm peels away to form a folded margin in the peripheral zone of the ventral surface, leaving a large opening which occupies nearly all the ventral surface of the cyst (Gocht 1968: pl. 25, figs 3–9; 1969: text-fig. 46c–e). At this stage the cyst attains the 'typical' morphology of *T. pelagica*.

The overall form of *Thalassiphora delicata* Williams & Downie 1966c emend. herein is very similar to that of *T. pelagica*. Three beautifully preserved specimens from the Upper Eocene part of the Bracklesham Beds exhibit a reflected tabulation of 4′, 1a, 5″, 4c, 5‴, 1p, 1⁗, and indicate that *T. delicata* is a dorsoventrally flattened cavate dinoflagellate cyst with several unusual characteristics (Figs 18, 20; Pl. 15, figs 3–5). The thin-walled relatively small central body is completely surrounded by the delicate periphragm, but the two layers are separated by a distinct pericoel except over the mid-dorsal area. The plate boundaries are defined by narrow thickenings of the periphragm, but they are absent from the area where the periphragm and endophragm are in contact. Most of the ventral surface of the periphragm is occupied by plates 1″ and 2‴, and the sulcal zone is displaced well to the left of the mid-ventral line. The large ventral opening in the periphragm noted in *T. pelagica* is also present in *T. delicata*, and in the latter species represents plate 1″. The significance of this opening has not been determined. It is difficult to envisage the displacement of this plate area being involved in archaeopyle formation since a 'conventional' dorsal precingular archaeopyle (3″) is developed in the endophragm and periphragm.

Although the described reflected tabulations of *T. pelagica* and *T. delicata* differ, the dorsal surface of *T. pelagica* (Gocht 1968: pl. 27, figs 2c, 3a; 1969: text-fig. 47)

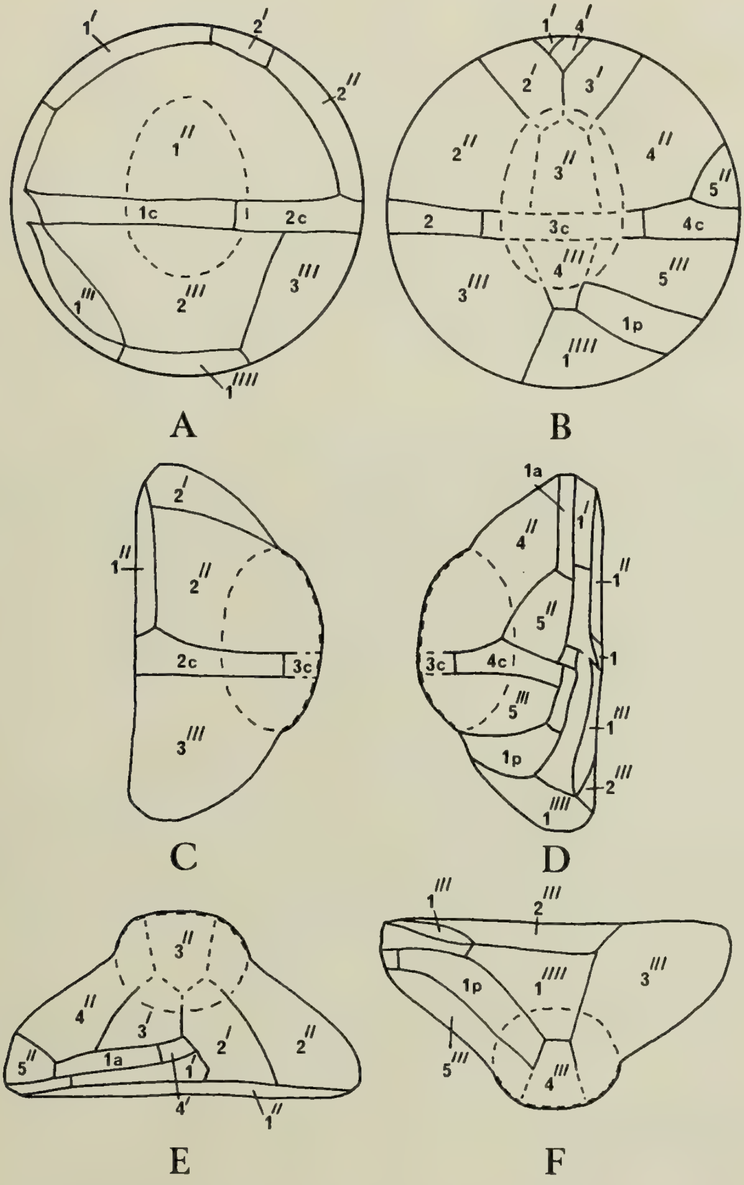

A
1′
2′
2″
1″
1c
2c
1‴
2‴
3‴
1⁗
B
1′
4′
2′
3′
2″
3″
4″
5″
2
3c
4c
4‴
3‴
5‴
1p
1⁗
C
2′
1″
2″
2c
3c
3‴
D
1a
1′
4″
1″
5″
3c
4c
1
5‴
1‴
1p
2‴
1⁗
E
3″
4″
3′
2′
2″
5″
1a
1′
4′
1″
F
1‴
2‴
1p
1⁗
3‴
5‴
4‴

Fig. 18. *Thalassiphora delicata* Williams & Downie 1966c emend. Diagrammatic representation of reflected tabulation. A. Ventral view. B. Dorsal view. C, D. Lateral views. E. Apical view. F. Antapical view. The central body (endophragm) is indicated by the broken line; plate boundaries represented by broken lines are inferred.

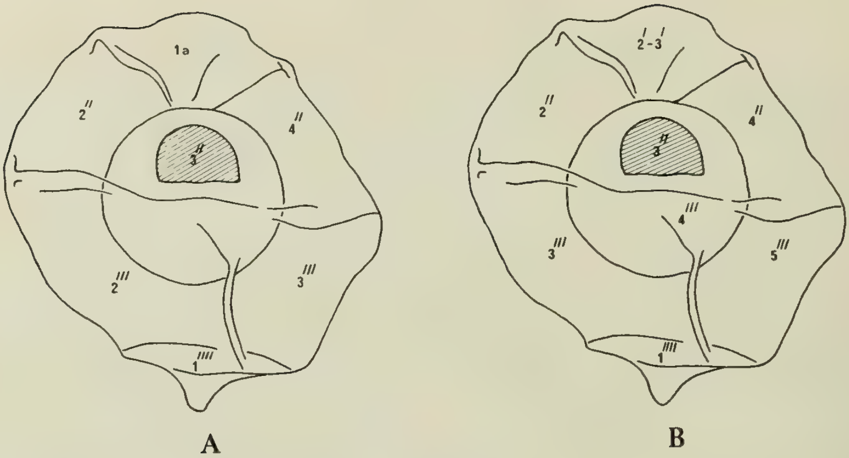


Fig. 19. *Thalassiphora pelagica* (Eisenack) Eisenack & Gocht 1960. Reflected tabulation of dorsal surface. A. Interpretation from Gocht (1968 : pl. 27, fig. 3a ; 1969 : text-fig. 47). B. Interpretation based on reflected tabulation of *Thalassiphora delicata* Williams & Downie 1966c emend. The precingular archaeopyle (3″) is represented by shading.

can be interpreted in terms of the reflected tabulation of *T. delicata* (Fig. 19). On this basis, the forms described by Gocht as initial and intermediate stages in the development of *T. pelagica* should be excluded from this species, and I agree with Drugg (1970 : 819) that some of these forms should be included in *Muratodinium* Drugg 1970.

If the concept of *Thalassiphora* is restricted to the original definition by Eisenack & Gocht (1960), together with the possible definition of plate areas, then the species assigned to *Thalassiphora*, e.g. *T. pelagica*, *T. delicata* and *T. reticulata* Morgenroth 1966b, exhibit a considerable range of texture and structure of the periphragm and endophragm. In this respect *T. pelagica* appears to be more closely related to forms such as *Muratodinium* and *Adnatosphaeridium* ? *patulum* Williams & Downie 1966c than to *T. delicata*, but in terms of the present accepted treatment of fossil dinoflagellate cyst taxa this relationship would be at supra-generic level.

Thalassiphora pelagica (Eisenack) Eisenack & Gocht 1960

Fig. 19 ; Pl. 16, figs 4–5

1938 *Bion pelagicum* Eisenack : 187 (*nom. nud.*).
1954 *Pterospermopsis pelagica* Eisenack : 71 ; pl. 12, figs 17–18.
1960 *Thalassiphora pelagica* (Eisenack) Eisenack & Gocht : 513 ; text-figs 1–3.

Dimensions. Observed range : periphragm 108 × 126 μ to 212 × 176 μ ; endophragm 60 × 66 μ to 98 × 94 μ ; length of keel up to 20 μ. (n = 9).

Remarks. Specimens here assigned to *T. pelagica* are dorsoventrally flattened and have a relatively thick-walled central body. The periphragm has a fibroreticulate appearance, and is separated from the endophragm by a distinct pericoel except over the mid-dorsal surface where the two layers are in contact. A small projection or 'keel' is developed in the periphragm at the antapex. In addition to the dorsal precingular archaeopyle (3″), a large opening is usually developed in the periphragm occupying most of the ventral surface.

OCCURRENCE. Lower, Middle and Upper Eocene.

PREVIOUS RECORDS. Upper Cretaceous (Maastrichtian) of Denmark (Wilson 1971); Lower Eocene of Belgium (Morgenroth 1966a, De Coninck 1972*), of northern France (Gruas-Cavagnetto 1970b, doubtful attribution), of north Germany (Morgenroth 1966a, Gocht 1968, 1969) and of the London Basin in southern England (Williams & Downie 1966c); Middle Eocene of northern France (Gruas-Cavagnetto 1971*) and of north Germany (Agelopoulos 1967, Gocht 1968, 1969); Upper Eocene of north Germany (Alberti 1961, as *Pterospermopsis* cf. *pelagica*; Agelopoulos 1967) and of East Prussia (Eisenack 1938, 1954, Eisenack & Gocht 1960); ? Upper Eocene of north Germany (Gocht 1968, 1969); Eocene, undifferentiated, of Argentina (Archangelsky 1968, 1969*), of Chile (Cookson & Cranwell 1967) and of Romania (Balteş 1969, as *T. delicata*); Middle Oligocene of north Germany (Gerlach 1961, Gocht 1968, 1969, Benedek 1972); Upper Oligocene of north Germany (Brosius 1963, Benedek 1972); ? Upper Oligocene of north Germany (Gerlach 1961); Oligocene, undifferentiated, of north Germany (Weiler 1956, as *Pterospermopsis* cf. *danica*) and of Romania (Balteş 1969, as *T. delicata*); Middle Miocene of north Germany (Gerlach 1961).

Thalassiphora delicata Williams & Downie 1966c emend. herein

Figs 18, 20; Pl. 16, figs 1–3

1966c *Thalassiphora delicata* Williams & Downie: 235; pl. 26, fig. 8.

EMENDED DIAGNOSIS. Central body subspherical or ellipsoidal, formed by the thin smooth endophragm. Periphragm dorsoventrally flattened with a subcircular or elliptical outline, smooth or with a minutely fenestrate appearance. Periphragm separated from the endophragm by a distinct pericoel, except over the mid-dorsal area where the two layers are in contact. Low simple linear thickenings of the periphragm are variably developed, and these define the plate boundaries. Reflected tabulation 4′, 1a, 5″, 4c, 5‴, 1p, 1⁗; archaeopyle precingular, formed by displacement of plate 3″. Distribution of the plates strongly asymmetrical. Most of the ventral surface is occupied by plates 1″ and 2‴. Sulcal zone offset well to the left of the mid-ventral line, occupying the lateral margin of the periphragm. A large opening is usually developed on the ventral surface of the periphragm, formed by displacement of plate 1″.

DIMENSIONS. Observed range: periphragm 75 × 62 μ to 112 × 120 μ; endophragm 36 × 30 μ to 60 × 46 μ. (n = 12).

REMARKS. *T. delicata* shows a variable development of linear thickenings of the periphragm defining the reflected tabulation. In some specimens only the cingular zone and a few of the other plate boundaries are recognizable; in others all the

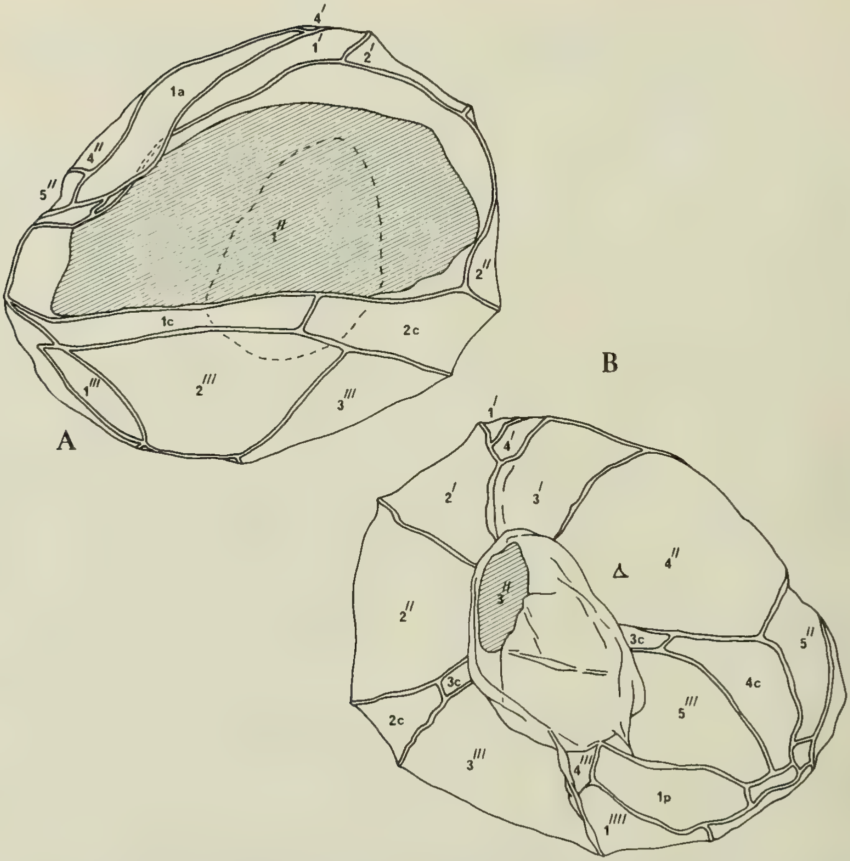


FIG. 20. *Thalassiphora delicata* Williams & Downie 1966c emend., reflected tabulation. A. Ventral view. The central body (endophragm) is indicated by the broken line; shading indicates the large ventral opening representing most of plate 1″. B. Dorsal view; the precingular archaeopyle (3″) is represented by shading. V.57766 (9); W56.

plates are clearly defined apart from those on the mid-dorsal area where the periphragm and endophragm are in contact (Figs 18B, 20B). There is some uncertainty in the reflected tabulation of the area where the sulcal zone crosses the cingular zone. The periphragm in this area frequently exhibits folds which tend to obscure the plate boundaries. Two small plate areas have been recognized which may include the anterior sulcal plate. A large posterior intercalary plate (1p) is developed to the left of the sulcal zone, bordered by plates 4‴, 5‴ and 1⁗. The development of a full reflected tabulation on the ventral surface allows the recognition of its unusual asymmetry, and the identification of the area of the large opening.

OCCURRENCE. Lower, Middle and Upper Eocene.

PREVIOUS RECORDS. Lower Eocene of Belgium (Pastiels 1948, as *Spore* inc. sed. Type-spécimen no. 3; De Coninck 1968, 1972*) and of the Hampshire and London

Basins in southern England (Williams & Downie 1966c) ; Middle Eocene of northern France (Gruas-Cavagnetto 1971*) ; Pleistocene of Norfolk, England (subsurface, presumably as reworking, Wall & Dale 1968b*).

Genus ***TURBIOSPHAERA*** Archangelsky 1968

In the original diagnosis of *Turbiosphaera*, Archangelsky (1968 : 408) defined the reflected tabulation as 1′, 6″, 6c, 6‴, (1p), 1⁗, with plate 1′ reflected by a large process or apical horn. In the two species here assigned to this genus the apical horn shows considerable proximal expansion. Although it could not be confirmed, these proximal expansions may well include apical processes situated around, and proximally united with, the apical horn.

Turbiosphaera galatea n. sp.

Pl. 15, figs 4–6

Derivation of Name. Greek *Γαλάτεια*, a sea nymph.

Diagnosis. Cyst body subcircular or oval in outline. Apical horn and delicate intratabular processes formed by the fibrous periphragm. Processes vary from discrete, with an undulating distal margin, to typically vague, due to their delicate appearance and the development of fibrous proximal membrane. They show considerable variation in breadth. Processes reflect the precingular, cingular, postcingular and antapical zones. Antapical process similar in form to the other processes, but longer, and proximally united with the postcingular processes. Apical horn broad, triangular in form, and showing considerable proximal expansion. Fibrous proximal membrane frequently unites processes in adjacent tabulation zones. Archaeopyle precingular, formed by displacement of plate 3″.

Holotype. B.M.(N.H.) Palaeont. slide V.57783 (4). Sample AB11, bed 2g, Bracklesham Beds, Lower Eocene, Alum Bay, Isle of Wight, England.

Dimensions. Holotype : overall $115 \times 84\,\mu$; cyst body $75 \times 63\,\mu$; length of processes up to $19\,\mu$; length of apical horn $23\,\mu$; length of antapical process $22\,\mu$. Observed range : overall $104 \times 68\,\mu$ to $130 \times 84\,\mu$; cyst body $60 \times 44\,\mu$ to $80 \times 75\,\mu$; length of processes up to $20\,\mu$; length of apical horn up to $30\,\mu$; length of antapical process up to $26\,\mu$. ($n = 10$).

Remarks. The considerable proximal expansion of the apical horn may include apical processes. The delicate appearance and typically vague definition of the processes precludes the determination of their exact number. When discrete processes are developed there appears to be one broad process per plate area, and more than one process per plate area when the processes are slender. The delicacy of its processes and the form of its apical horn distinguish *T. galatea* n. sp. from *T. filosa* (Wilson) Archangelsky 1968.

Occurrence. Lower Eocene.

Turbiosphaera magnifica n. sp.

Pl. 15, figs 7–9

Derivation of Name. Latin, *magnificus*, magnificent.

Diagnosis. Cyst body subcircular or oval in outline. Apical horn and intratabular processes formed by the fibrous periphragm. Processes variable in breadth, with an undulating distal margin. There is one process per reflected plate area. Apical horn long, broad-based, triangular in form and showing considerable proximal expansion. Pre- and postcingular processes typically flattened parallel to the long axis of the cyst body. Cingular processes flattened parallel to the short axis of the cyst body. Cingular zone slightly helicoid. Antapical process longer than the other processes, distally expanded, and frequently showing a short distal projection. Very slender processes may be present between the primary precingular and cingular processes. Precingular processes situated close to, and sometimes united with, the proximal expansions of the apical horn. Postcingular processes situated close to, and proximally united with, the antapical process. Reflected tabulation 1′, 6″, 6c, 5‴, 1⁗; archaeopyle precingular, formed by displacement of plate 3″.

Holotype. B.M.(N.H.) Palaeont. Slide V.57756 (7). Sample W40, bed 11, Bracklesham Beds, Middle Eocene, Whitecliff Bay, Isle of Wight, England.

Dimensions. Holotype: overall 144 × 62 μ; cyst body 74 × 46 μ; length of processes up to 26 μ; length of apical horn 38 μ; length of antapical process 36 μ. Observed range: overall 110 × 62 μ to 148 × 80 μ; cyst body 56 × 46 μ to 80 × 62 μ; length of processes up to 34 μ; length of apical horn up to 48 μ; length of antapical process up to 38 μ. (n = 10).

Remarks. The considerable proximal expansion of the apical horn may include apical processes. The development of very slender processes between the primary precingular and cingular processes is also a feature of Forma F of Evitt (1961 : 392; pl. 6, figs 1–5; pl. 7, figs 1–2). The close affinity between the latter form and *Turbiosphaera filosa* has been noted by Wilson (1967a : 66) and Archangelsky (1968 : 410). The processes are arranged in three discrete groups: apical horn and precingular processes, cingular processes, antapical and postcingular processes. This feature and the form of its apical horn distinguishes *T. magnifica* n. sp. from *T. filosa* (Wilson) Archangelsky 1968 and *T. galatea* n. sp. It is further distinguished from *T. galatea* by having a longer apical horn and more clearly defined processes.

Occurrence. Middle Eocene.

PERIDINIACEAN GROUP

Genus ***DEFLANDREA*** Eisenack 1938 emend. Williams & Downie 1966c

Deflandrea phosphoritica Eisenack 1938

Pl. 17, fig. 1

1938 *Deflandrea phosphoritica* Eisenack : 187; fig. 6.

DIMENSIONS. Observed range : periphragm, length 80–132 μ, breadth 72–100 μ; endophragm, length 50–78 μ, breadth 60–84 μ. (n = 24).

OCCURRENCE. Lower, Middle and Upper Eocene.

PREVIOUS RECORDS. Palaeocene of northern France (Chateauneuf & Gruas-Cavagnetto 1968*) and of Russia (Alberti 1959) ; Lower Eocene of Belgium (Reissinger 1950, Morgenroth 1966a, Gruas-Cavagnetto 1968), of northern France (Chateauneuf & Gruas-Cavagnetto 1968*), of north Germany (Morgenroth 1966a, Gocht 1969), of northern Spain (Caro 1973), of Russia (Alberti 1959) and of the Hampshire and London Basins in southern England (Williams & Downie 1966c, Downie, Husain & Williams 1971) ; ? Lower Eocene of Victoria, Australia (Deflandre & Cookson 1955) ; Middle Eocene of north Germany (Agelopoulos 1967, Gocht 1969) ; Upper Eocene of Belgium (Rozen 1965), of East Prussia (Eisenack 1938, 1954), of northern France (Chateauneuf & Gruas-Cavagnetto 1968*), of north Germany (Klumpp 1953, Alberti 1959, Agelopoulos 1967), of the Hampshire Basin (Gruas-Cavagnetto 1970a*) and of Victoria (Cookson & Eisenack 1965) ; ? Upper Eocene of north Germany (Gocht 1969) ; Eocene, undifferentiated, of Romania (Balteş 1969), of Russia (Alberti 1959) and of Western Australia (Cookson & Eisenack 1961) ; Upper Eocene–Lower Oligocene of Russia (Chiguryaeva 1956, as Algae ? (Peridineae) ; Vozzhennikova 1967) ; Lower Oligocene of northern France (Chateauneuf & Gruas-Cavagnetto 1968*) ; Middle Oligocene of northern France (Chateauneuf & Gruas-Cavagnetto 1968*) and of north Germany (Maier 1959, Alberti 1959, Gerlach 1961, Gocht 1969, Benedek 1972) ; Upper Oligocene of north Germany (Maier 1959, Alberti 1959, Gerlach 1961, Brosius 1963, Benedek 1972) ; Oligocene, undifferentiated, of Romania (Balteş 1969) ; Lower Tertiary, undifferentiated, of Russia (Alberti 1959), of Spitzbergen (Manum 1960) and of Tierra del Fuego, Argentina (Baldis 1966) ; Miocene, undifferentiated, of Romania (Balteş 1967*).

Deflandrea depressa Morgenroth 1966a

Pl. 16, fig. 6

1966a *Deflandrea depressa* Morgenroth : 8 ; pl. 1, fig. 2.

DESCRIPTION. A single specimen of *D. depressa* has been recorded in this study. The periphragm and endophragm are very thin. The epitractal portion of the periphragm tapers from the cingular zone to form a large apical horn ; the antapical margin of the periphragm is produced into two distinct horns. The helicoid cingular zone is best defined on the ventral surface ; horns ornamented with a sparse covering of fine granules and the area of the periphragm in contact with the endophragm crossed by numerous delicate longitudinal wrinkles.

DIMENSIONS. Periphragm, length 70 μ, breadth 32 μ ; endophragm, length 32 μ, breadth 32 μ. (n = 1).

OCCURRENCE. Middle Eocene.

PREVIOUS RECORDS. Lower Eocene of north Germany (Morgenroth 1966a), of Belgium (De Coninck 1968, 1972*) and of northern France (Chateauneuf & Gruas-Cavagnetto 1968*).

Deflandrea wetzeli Morgenroth 1966a

Pl. 17, fig. 4

1966a *Deflandrea wetzeli* Morgenroth : 9 ; pl. 1, figs 4–5.

DESCRIPTION. Outline of periphragm broadly oval, modified by the development of a short apical horn and two short antapical horns. Periphragm ornamented with short blunt or acuminate projections, which may be proximally united on the margins of the cingular zone. Apart from the area immediately below the horns, the endophragm lies very close to, or in contact with, the periphragm.

DIMENSIONS. Observed range : periphragm, length 46–88 μ, breadth 35–60 μ ; endophragm, length 31–56 μ, breadth 35–56 μ. (n = 36).

OCCURRENCE. Lower, Middle and Upper Eocene.

PREVIOUS RECORDS. Lower Eocene of north Germany (Morgenroth 1966a) and of Belgium (Pastiels 1948, as *Peridinium* cf. *galeatum* – pl. 5, fig. 17 only ; De Coninck 1968).

Genus ***KISSELEVIA*** Vozzhennikova 1967

In the original description of this genus (as *Kisselovia* nom. nud.), Vozzhennikova (1963) noted the presence of an internal body. In a later paper (Vozzhennikova 1967), however, she considered this statement erroneous and stated that no internal body was present. Examination of her illustration of *Kisselevia ornata* (Vozzhennikova 1967 : pl. 43, fig. 1) and the specimens here assigned to *K. insolens* n. sp. suggests that an outer periphragm and an inner capsule (endophragm) are distinguishable. The reticulate 'armour' which is characteristic of the genus consists of a complex mesh of interconnected trabeculae distally uniting the short processes distributed over the periphragm. In *K. insolens* n. sp. this attains the appearance of a fenestrate membrane. In the latter species only the dorsal surface reflected tabulation has been determined and this is clearly peridiniacean.

Confirmation of the separation of the periphragm and endophragm in the Russian species of *Kisselevia* would suggest a close affinity between this genus and *Wetzeliella* Eisenack 1938 emend. Williams & Downie 1966b. This would favour the establishment of *Kisselevia* as a subgenus of *Wetzeliella* to accommodate existing species of *Kisselevia* and species now assigned to *Wetzeliella* (*Wetzeliella*) Eisenack 1938 in which the processes are distally united by membranes or trabeculae (e.g. *W.* (*W.*) *tenuivirgula* Williams & Downie 1966b).

Kisselevia insolens n. sp.

Pl. 18, figs 1–2

DERIVATION OF NAME. Latin, *insolens*, odd, strange, with reference to the unusual fenestrate 'shell' which distally unites the processes in this species.

Diagnosis. Overall outline rounded pentagonal or rounded tetragonal. Periphragm produced into five horns, one apical, two lateral and two antapical. Right antapical horn typically slightly shorter than the left. Separation of the periphragm and endophragm may be distinguishable at the base of each horn. Thick short processes are developed over the periphragm, and arranged in simulate complexes. Processes in each complex are distally united by a thick strong fenestrate membrane whose outline and area are similar to those of the underlying plate. Fenestrations in the membrane variable in size and shape (circular, subcircular or rounded polygonal). Adjacent areas of fenestrate membrane united by thick bars. The resulting outer layer has the appearance of a strong fenestrate 'shell'. Reflected tabulation of the form 4', 3a, 7'', 5''', 2'''' ; archaeopyle intercalary, formed by displacement of plate 2a.

Holotype. B.M.(N.H.) Palaeont. slide V.57774 (4). Sample AB4, bed 2c, Bracklesham Beds, Lower Eocene, Alum Bay, Isle of Wight, England.

Dimensions. Holotype: overall $118 \times 115\ \mu$. Observed range: overall $112 \times 112\ \mu$ to $148 \times 134\ \mu$. (n = 4).

Remarks. Although the basic reflected tabulation in *K. insolens* n. sp. is considered to be comparable to that of *Wetzeliella* Eisenack 1938 emend. Williams & Downie 1966b, only the dorsal surface reflected tabulation has been precisely determined. The cingular zone is not marked by areas of fenestrate membrane ; the areas of membrane over the pre- and postcingular zones are united across the cingular zone by thick bars. The presence of a strong fenestrate outer 'shell' distinguishes *K. insolens* from described species of *Kisselevia* which are characterized by the presence of a relatively delicate network of distal trabeculae. *K. insolens* does show some overall similarity to the single specimen attributed to *Wetzeliella* (*W.*) *tenuivirgula* var. *crassoramosa* Williams & Downie 1966b in this study, but in the latter form the processes are distally united by a network of extremely thick trabeculae rather than a fenestrate 'shell'.

Occurrence. Lower Eocene.

Genus ***LEJEUNIA*** Gerlach 1961

Lejeunia hyalina Gerlach 1961

Pl. 17, fig. 5

1961 *Lejeunia hyalina* Gerlach : 169 ; pl. 26, figs 10–11.

Dimensions. Observed range: overall $56 \times 62\ \mu$ to $100 \times 108\ \mu$. (n = 6).

Remarks. The only tabulation features observed are the cingular zone and a poorly defined sulcal zone indicated by folds or thickenings of the cyst wall, and a simple archaeopyle on the dorsal surface which appears to be intercalary in position.

Occurrence. Lower and Middle Eocene.

Previous Records. Palaeocene of Russia (Vozzhennikova 1967) ; Lower Eocene of Belgium (De Coninck 1968) and of north Germany (Gocht 1969) ; Middle Oligocene of north Germany (Benedek 1972) ; Upper Oligocene of north Germany (Gerlach 1961).

Genus ***PALAEOCYSTODINIUM*** Alberti 1961

Palaeocystodinium golzowense Alberti 1961

Pl. 16, fig. 7

1961 *Palaeocystodinium golzowense* Alberti : 20 ; pl. 7, figs 10–12 ; pl. 12, fig. 16.

Dimensions. Observed range : overall length of periphragm 156–220 μ ; endophragm 60 × 25 μ to 64 × 50 μ. (n = 4).

Occurrence. Lower, Middle and Upper Eocene.

Previous Records. Upper Cretaceous (Maastrichtian) and ? Palaeocene of Gabon, west Africa (Malloy 1972) ; Palaeocene of South Dakota, U.S.A. (Stanley 1965) ; Lower Eocene of Belgium (De Coninck 1968, 1972*) and of France (Gruas-Cavagnetto 1970b*) ; Upper Eocene of north Germany (Alberti 1961) ; Middle Oligocene of north Germany (Alberti 1961, Benedek 1972) ; Upper Oligocene of north Germany (Alberti 1961, Brosius 1963, as *Netrelytron* sp. ; Benedek 1972).

Genus ***PHTHANOPERIDINIUM*** Drugg & Loeblich 1967

The genus was originally defined by Drugg & Loeblich (1967). The type species, *P. amoenum* Drugg & Loeblich 1967, from the Oligocene of Mississippi, U.S.A., has a basic reflected tabulation of 4′, 3a, 7″, 5c, 5‴, 1⁗, and subdivision of the sulcal zone. Three new species of *Phthanoperidinium* are here recorded – *P. alectrolophum*, *P. echinatum* and *P. tritonium*. No indication of individual plate areas has been recognized in the cingular and sulcal zones of these, the reflected tabulation being 4′, 3a, 7″, 5‴, 1⁗ (Fig. 21). Three other described taxa from Palaeogene sediments are here transferred to the genus *Phthanoperidinium* on the basis of their overall morphology and reflected tabulation :

Phthanoperidinium comatum (Morgenroth 1966b) n. comb. = *Peridinium comatum* Morgenroth 1966b : 1 ; pl. 1, figs 1–2. Lower Oligocene, north Germany.

Phthanoperidinium eocenicum (Cookson & Eisenack 1965) n. comb. = *Peridinium eocenicum* Cookson & Eisenack 1965 : 119 ; pl. 11, figs 1–5. Upper Eocene, Victoria, Australia.

Phthanoperidinium resistente (Morgenroth 1966a) n. comb. = *Peridinium resistente* Morgenroth 1966a : 5 ; pl. 2, figs 1–2. Lower Eocene, north Germany.

Three species assigned to *Hystrichogonyaulax* Sarjeant 1969 by Benedek (1972) – *Hystrichogonyaulax* sp., *H. coreoides* and *H. polytrix*, recorded from the Middle Oligocene of north Germany – are possibly referable to *Phthanoperidinium* on the basis of their morphology and probable archaeopyle position. However, the reflected tabulation of *H. coreoides* as described by Benedek (1972) does not conform with that of *Phthanoperidinium*, while in *Hystrichogonyaulax* sp. and *H. polytrix* the reflected tabulation has not been determined.

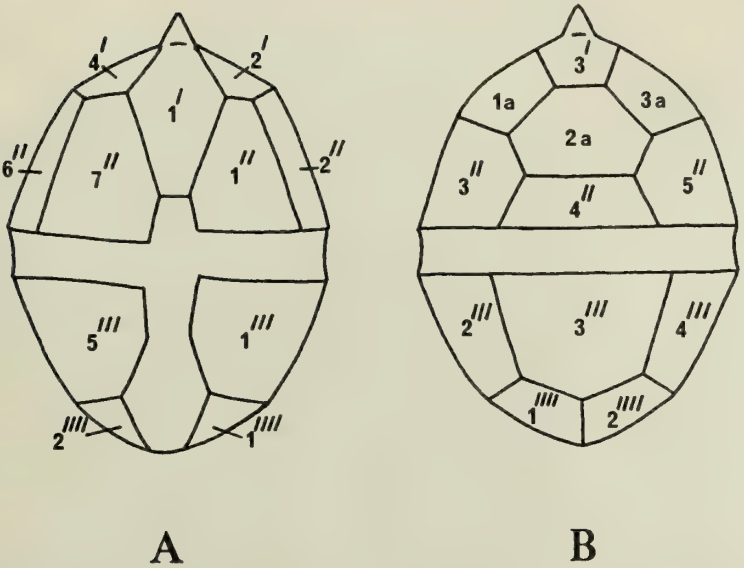


Fig. 21. Diagrammatic representation of the reflected tabulation of *Phthanoperidinium* Drugg & Loeblich 1967 as exhibited by forms from the Bracklesham Beds. A. Ventral view. B. Dorsal view.

Phthanoperidinium alectrolophum n. sp.

Fig. 23A; Pl. 17, figs 10–11

Derivation of Name. Greek ἀλεκτορόλοφος, cockscomb, with reference to the form of the sutural crests.

Diagnosis. Cyst body has a smooth surface, and a subcircular or rounded polygonal outline modified by a short blunt apical horn. Plate boundaries marked by thin smooth sutural crests of variable height. Undulating distal margin of crests frequently thickened, bearing numerous short solid spines. Cingular zone clearly defined, and slightly helicoid. Reflected tabulation 4′, 3a, 7″, 5‴, 2⁗; archaeopyle intercalary, formed by displacement of plate 2a.

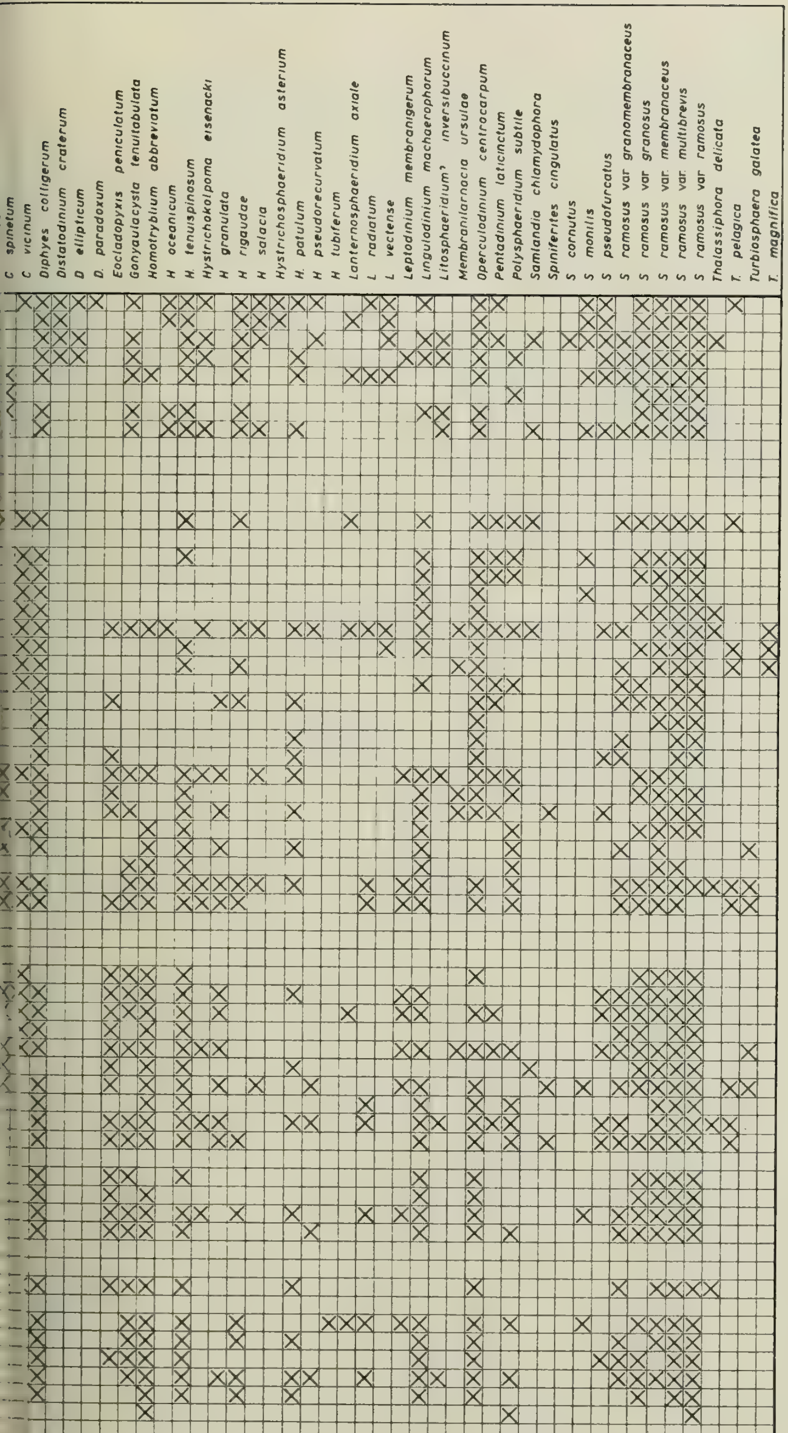
Holotype. B.M.(N.H.) Palaeont. slide V.57791 (13). Sample AB40, bed 19, Bracklesham Beds, Upper Eocene, Alum Bay, Isle of Wight, England.

Dimensions. Holotype: overall 59 × 48 μ; height of crests up to 7 μ; length of spines up to 2 μ. Observed range: overall 40 × 30 μ to 60 × 56 μ; height of crests up to 7 μ; length of spines up to 2 μ. (n = 6).

Remarks. The sutural crests in *Phthanoperidinium alectrolophum* n. sp. are similar in form to those of *P. campoense* Caro 1973 (incorrectly cited as *Phtanoperidinium*) and *P. eocenicum* (Cookson & Eisenack 1965) n. comb. In *P. campoense* the crests are described as being surmounted by short irregularly distributed projections, as opposed to the relatively dense regular spine distribution in *P. alectrolophum*. The crests in *P. eocenicum* do not show a distal thickening, and their distal

SUCCESSION			TAXA	*Achilleodinium biformoides*	*Achomosphaera alcicornu*	*A. membraniphora*	*A ramulifera*	*Adnatosphaeridium multispinosum*	*A. robustum*	*A. vittatum*	*Araneosphaera araneosa*	*Areoligera coronata*	*A. cf. coronata*	*A. medusettiformis*	*A. cf medusettiformis*	*A senonensis*	*A. cf. senonensis*	*A sentosa*	*A tauloma*	*A undulata*	*Areosphaeridium arcuatum*	*A. diktyoplokus*	*A. multicornutum*	*Cannosphaeropsis reticulensis*	*Chiropteridium cf. dispersum*	*Cordosphaeridium exilimurum*	*C. fibrospinosum*	*C gracilis*	*C inodes*	*C? minimum*	*C. multispinosum*	*Cyclonephelium divaricatum*	*C. exuberans*	*C.*
CLAYS	19	c	58	X		X	X	X		X	X							X	X	X	X	X	X					X	X	X				
			57			X	X	X		X	X								X	X	X							X	X					
			56	X	X	X	X	X			X							X	X	X	X	X	X					X		X				
		b	55			X	X	X			X									X	X	X		X						X				
		a	54				X	X												X	X	X						X	X				X	
SAND – ROCK	18		53					X										X										X						
SANDY CLAYS	17		52	X		X	X	X																				X						
			51	X			X	X													X	X				X		X	X				X	
SANDS	16		50																															
			49																															
			48																															
SANDS	15		47																															
SANDY CLAYS	14		46	X		X	X	X		X								X				X				X		X	X				X	
SANDS	13		45					X														X												
SANDY CLAYS	12		44	X			X	X		X	X											X						X	X					
			43				X	X		X	X																		X					
LAMINATED BEDS	11		42				X	X		X	X																	X	X				X	
			41	X			X	X		X																							X	
			40	X	X	X	X	X		X	X		X		X						X	X			X	X			X			X	X	
GREENSANDS	10	b	39	X			X	X			X											X			X			X	X				X	
			38	X			X	X							X							X			X			X	X			X	X	
		a	37	X			X	X																		X		X	X				X	
			36	X			X	X																	X				X					
			35	X			X	X																	X	X			X					
			34	X			X	X																		X			X				X	
			33	X			X	X			X																	X	X					
			32	X	X		X	X										X	X			X				X		X	X					
			31	X			X	X										X	X						X				X					
			30	X			X	X		X									X			X			X			X	X	X	X	X		
LAMINATED BEDS	9	c	29	X			X	X																	X				X				X	
		b	28A				X	X		X			X																X				X	
		a	28				X	X							X												X	X	X				X	
			27	X			X	X		X					X							X					X		X				X	
			26A				X	X		X			X															X	X				X	
LIGNITE & UNDERCLAY	8		26																															
			25B																															
			25A																															
LAMINATED BEDS	7		25				X	X		X					X												X	X			X		X	
			24				X	X																		X	X							
			23	X			X	X					X									X						X	X			X		
GREENSAND	6		22A				X	X																					X					
SANDY CLAYS	5		22				X	X					X															X	X		X	X		
			21				X	X																					X					
			20	X			X	X		X			X		X		X									X		X	X		X	X	X	
			19				X	X	X						X													X			X		X	X
			18				X	X	X				X		X		X									X	X	X	X			X	X	X
LAMINATED BEDS	4		17	X			X	X		X			X		X		X							X		X	X	X	X		X	X	X	X
SANDS	3		16																															
LAMINATED BEDS	2		15				X	X					X		X		X									X	X		X		X	X	X	
			14				X	X					X	X	X	X	X									X	X	X			X		X	
			13		X		X	X		X		X	X	X	X	X	X										X	X	X		X	X	X	X
			12				X	X		X					X		X											X			X	X		
			11																															
			10																															
			9				X	X		X			X		X		X										X	X	X		X	X		
			8																															
SANDY CLAYS	1		7				X	X	X			X	X		X													X				X		X
			6				X																	X			X		X					
			5				X	X	X	X			X		X		X									X	X	X	X				X	
			4		X		X	X	X				X	X	X		X									X	X	X	X				X	
			3				X	X	X						X											X	X	X	X					
			2					X	X				X		X													X					X	
			1																															

Fig. 22. Distribution of dinoflagellate cyst taxa assigned to the Gonyau



ceæ Group in the Bracklesham Beds at Whitecliff Bay, Isle of Wight.

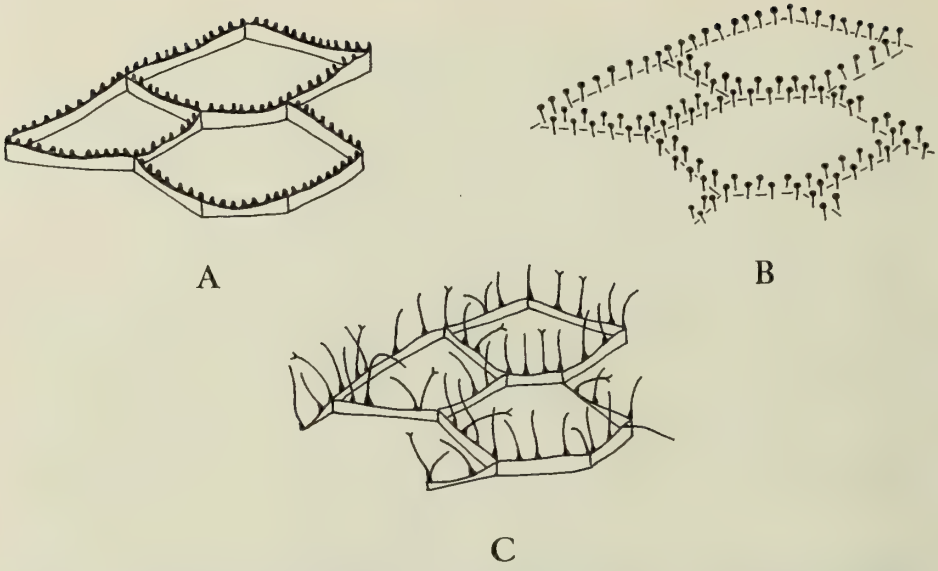


FIG. 23. Diagrammatic representation of the ornament in three new species of *Phthanoperidinium*. A. *P. alectrolophum* n. sp. B. *P. echinatum* n. sp. C. *P. tritonium* n. sp.

margin is described as being ornamented with evenly spaced granules and small tubercles, or sparsely denticulate. This species is further distinguished from *P. alectrolophum* by the presence of an antapical horn.

OCCURRENCE. Upper Eocene.

Phthanoperidinium echinatum n. sp.

Fig. 23B ; Pl. 17, figs 8–9, 12

DERIVATION OF NAME. Latin, *echinatus*, prickly, spiny, with reference to the form of the spinate ornament.

DIAGNOSIS. Cyst body has a smooth surface, and a subcircular or rounded polygonal outline modified by a short blunt apical horn. Plate boundaries accentuated by a distinctive ornament concentrated at the plate margins, consisting of short hair-like projections, each with a bulbous spherical distal termination. Cingular zone clearly defined and slightly helicoid. Reflected tabulation $4'$, 3a, $7''$, $5'''$, $2''''$; archaeopyle intercalary, formed by displacement of plate 2a.

HOLOTYPE. B.M.(N.H.) Palaeont. slide V.57755 (4). Sample W39, bed 10b, Bracklesham Beds, Middle Eocene, Whitecliff Bay, Isle of Wight, England.

DIMENSIONS. Holotype : overall $29 \times 22\ \mu$; length of spines up to $2\ \mu$. Observed range : overall $26 \times 22\ \mu$ to $48 \times 42\ \mu$; length of spines up to $3\ \mu$. $(n = 26)$.

REMARKS. The majority of the recorded specimens are complete or exhibit an intercalary archaeopyle formed by the displacement of plate 2a. A few specimens have been observed with plate $4''$ displaced as well as plate 2a, probably due to sutural weakness. The distinctive ornament of *P. echinatum* distinguishes this species from all described species of *Phthanoperidinium*.

OCCURRENCE. Lower, Middle and Upper Eocene.

Phthanoperidinium tritonium n. sp.

Figs 23C, 24; Pl. 17, figs 2–3, 6–7

DERIVATION OF NAME. Latin, *Triton*, a sea god.

DIAGNOSIS. Cyst body has a smooth surface, and a subcircular or rounded polygonal outline modified by a short blunt apical horn. Plate boundaries marked by thin smooth sutural crests of variable height, bearing erect or curved solid spines which may be distally simple or bifurcate. Cingular zone clearly defined and distinctly helicoid. Reflected tabulation $4'$, 3a, $7''$, $5'''$, $2''''$; archaeopyle intercalary, formed by displacement of plate 2a.

HOLOTYPE. B.M.(N.H.) Palaeont. slide V.57756 (14). Sample W40, bed 11, Bracklesham Beds, Middle Eocene, Whitecliff Bay, Isle of Wight, England.

DIMENSIONS. Holotype: cyst body $44 \times 37\ \mu$; length of spines up to $7\ \mu$. Observed range: cyst body $30 \times 26\ \mu$ to $56 \times 46\ \mu$; length of spines up to $13\ \mu$. ($n = 22$).

REMARKS. In some specimens, in addition to plate 2a (the operculum), plate $4''$ is also displaced (Pl. 17, fig. 7), and in one specimen all three intercalary plates have

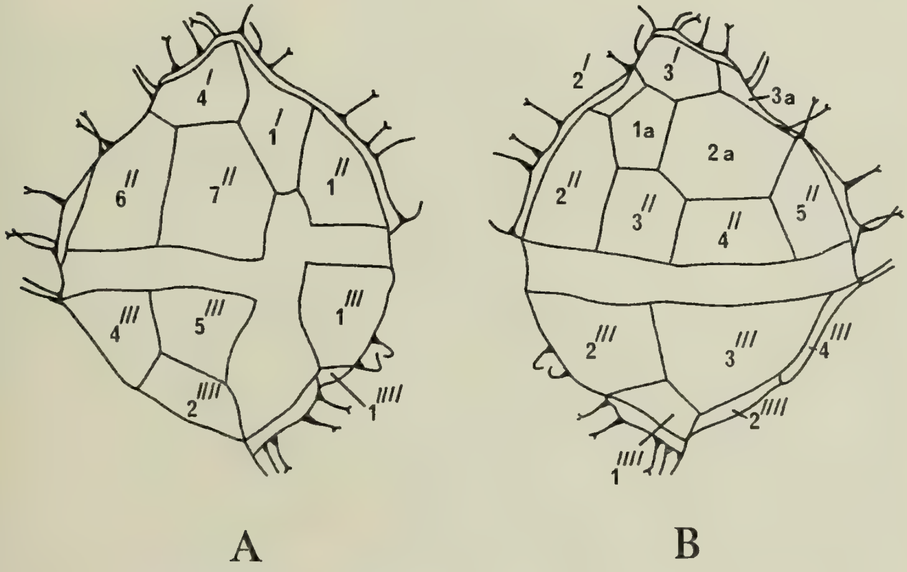


FIG. 24. *Phthanoperidinium tritonium* n. sp. Reflected tabulation of holotype. A. Ventral view. B. Dorsal view. V.57756 (14); W40.

been lost, probably owing to sutural weakness. In overall form *Phthanoperidinium tritonium* n. sp. is similar to *P. comatum* (Morgenroth 1966b) n. comb., which is distinguished by its consistently longer spines (maximum 28 μ, majority 14–22 μ). The sutural crests in *P. tritonium* are similar to those of *P. alectrolophum* n. sp., though in the latter species the crests bear numerous short simple spines, while in *P. tritonium* they are longer, more widely spaced, and may be distally bifurcate.

Occurrence. Lower, Middle and Upper Eocene.

Genus ***WETZELIELLA*** Eisenack 1938 emend. Williams & Downie 1966b

Subgenus ***WETZELIELLA*** Eisenack 1938

Wetzeliella (Wetzeliella) articulata Eisenack 1938

Pl. 18, fig. 3

1938 *Wetzeliella articulata* Eisenack : 186 ; fig. 4.
1961 *Wetzeliella* (*Wetzeliella*) *articulata* Eisenack ; Alberti : 7.

Dimensions. Observed range: periphragm 78 × 78 μ to 164 × 164 μ; endophragm 66 × 64 μ to 102 × 102 μ. (n = 40).

Occurrence. Lower, Middle and Upper Eocene.

Previous Records. Palaeocene of Victoria, Australia (Cookson 1956, doubtful attribution) ; Uppermost Palaeocene of north Germany (Alberti 1961) ; Palaeocene–Lower Eocene of New Zealand (Wilson 1967c, 1968a*) ; Lower Eocene of Belgium (De Coninck 1965, 1967*, 1972* ; Morgenroth 1966a), of northern France (Chateauneuf & Gruas-Cavagnetto 1968, Gruas-Cavagnetto 1970b*), of north Germany (Alberti 1961, Morgenroth 1966a), of northern Spain (Caro 1973) and of the Hampshire and London Basins in southern England (Williams & Downie 1966b) ; Middle Eocene of north Germany (Klumpp 1953, Agelopoulos 1967) ; Upper Eocene of northern France (Chateauneuf & Gruas-Cavagnetto 1968), of north Germany (O. Wetzel 1935, as *Peridinium* sp. indet. ; Klumpp 1953, Alberti 1961, Agelopoulos 1967), of East Prussia (Eisenack 1938, 1954) and of Russia (Alberti 1961, Vozzhennikova 1967) ; ? Upper Eocene of north Germany (Gocht 1969) ; Lower Oligocene of northern France (Chateauneuf & Gruas-Cavagnetto 1968) and of Russia (Vozzhennikova 1967) ; Middle Oligocene of northern France (Chateauneuf & Gruas-Cavagnetto 1968) and of north Germany (Alberti 1961, Gerlach 1961, Gocht 1969) ; Upper Oligocene of north Germany (Alberti 1961, Gerlach 1961, Brosius 1963) ; ? Middle Miocene of north Germany (Gerlach 1961).

Wetzeliella (Wetzeliella) coleothrypta Williams & Downie 1966b

Pl. 18, fig. 4

1966b *Wetzeliella* (*Wetzeliella*) *coleothrypta* Williams & Downie : 185 ; pl. 18, figs 8–9 ; text-fig. 47.

Dimensions. Observed range: periphragm 100 × 84 μ to 150 × 146 μ; endophragm 60 × 50 μ to 116 × 98 μ. (n = 21).

Remarks. In typical forms the processes in each simulate complex are distally united by a thin membrane similar in outline and area to the underlying plate. Other specimens show a reduction in the areas of distal membrane. These forms appear to be transitional to *W.* (*W.*) *clathrata* Eisenack 1938 in which adjacent processes are distally united by narrow ribbons or 'lists'.

Occurrence. Lower, Middle and Upper Eocene.

Previous Records. Lower Eocene of New Zealand (Wilson 1967c), of northern Spain (Caro 1973) and of the London Basin in southern England (Williams & Downie 1966b, Downie, Husain & Williams 1971); Middle Eocene of northern France (Gruas-Cavagnetto 1971*).

Wetzeliella (Wetzeliella) condylos Williams & Downie 1966b

Pl. 18, fig. 5

1966b *Wetzeliella* (*Wetzeliella*) *condylos* Williams & Downie: 193; pl. 20, figs 1–2.

Dimensions. Observed range: periphragm 74 × 86 μ to 100 × 100 μ; endophragm 54 × 60 μ to 76 × 80 μ. (n = 4).

Remarks. The periphragm forms short reduced lateral and antapical horns. The curved apical margin is sometimes developed into a low apical horn.

Occurrence. Lower Eocene.

Previous Records. Lower Eocene of the London Basin in southern England (Williams & Downie 1966b, Downie, Husain & Williams 1971).

Wetzeliella (Wetzeliella) homomorpha Deflandre & Cookson 1955

Pl. 19, fig. 1

1955 *Wetzeliella homomorpha* Deflandre & Cookson: 254; pl. 5, fig. 7; text-fig. 19.
1966a *Wetzeliella* (*Wetzeliella*) *homomorpha* Deflandre & Cookson; Morgenroth: 10; pl. 1, figs 8–9.

Dimensions. Observed range: overall (including processes) 66 × 60 μ to 85 × 86 μ; periphragm 46 × 44 μ to 78 × 74 μ. (n = 15).

Occurrence. Lower, Middle and Upper Eocene.

Previous Records. Palaeocene of New Zealand (Wilson 1967c), of Tasmania (Cookson & Eisenack 1967a), of northern France (Chateauneuf & Gruas-Cavagnetto 1968) and of northern Spain (Caro 1973); Lower Eocene of Belgium (Pastiels 1948, as *Hystrichosphaeridium geometricum*; De Coninck 1965, 1967*, 1968, 1972*, Morgenroth 1966a, Gruas-Cavagnetto 1968), of northern France (Gruas-Cavagnetto 1968, 1970b, Chateauneuf & Gruas-Cavagnetto 1968), of north Germany (Morgenroth 1966a), of northern Spain (Caro 1973), of the Hampshire and London Basins in southern England (Williams & Downie 1966b, Downie, Husain & Williams 1971*) and of Victoria, Australia (Deflandre & Cookson 1955); Middle Eocene of northern France (Gruas-Cavagnetto 1971*); Upper Eocene, and Lower and Middle Oligocene of northern France (Chateauneuf & Gruas-Cavagnetto 1968); ? Oligocene of Victoria (Cookson 1953, as *Hystrichosphaeridium geometricum*).

Wetzeliella (Wetzeliella) lunaris Gocht 1969

Pl. 19, fig. 2

1969 *Wetzeliella* (*Wetzeliella*) *lunaris* Gocht: 13; pl. 10, figs 1–3; text-fig. 6.

DIMENSIONS. Observed range: periphragm 78 × 74 μ to 146 × 140 μ; endophragm 54 × 56 μ to 90 × 84 μ. (n = 12).

REMARKS. In *W.* (*W.*) *lunaris* four of the five horns are well developed – the apical, two lateral and the left antapical. The right antapical horn is considerably reduced. The endophragm is subcircular to rounded tetragonal in outline, and its margin is always separated from the periphragm by a narrow pericoel.

OCCURRENCE. Lower and Middle Eocene.

PREVIOUS RECORDS. Lower Eocene of Belgium (Pastiels 1948, as *Hystrichosphaeridium articulatum*, pl. 4, figs 13, 17 only; De Coninck 1965, as *W. articulata*, pl. 1, figs 3–6 only; Gruas-Cavagnetto 1968, as *W. articulata*), of north Germany (Gocht 1969) and of the Hampshire and London Basins in southern England (Williams & Downie 1966b, as *W.* (*W.*) *symmetrica* var. *lobisca*; Downie, Husain & Williams 1971).

Wetzeliella (Wetzeliella) meckelfeldensis Gocht 1969

Pl. 19, fig. 5

1969 *Wetzeliella* (*Wetzeliella*) *meckelfeldensis* Gocht: 15; pl. 10, figs 12–15.

DIMENSIONS. Observed range: periphragm 78 × 78 μ to 166 × 150 μ; endophragm 58 × 54 μ to 98 × 92 μ. (n = 6).

REMARKS. In *W.* (*W.*) *meckelfeldensis* only four horns are developed – one apical, two lateral, and a single antapical horn which is slightly offset to the left when viewed from the dorsal surface. The endophragm has an oval outline, and apart from the area at the base of each horn, it is typically in contact with the periphragm.

OCCURRENCE. Lower Eocene.

PREVIOUS RECORDS. Lower Eocene of north Germany (Gocht 1969) and of the Hampshire and London Basins in southern England (Williams & Downie 1966b, as *W.* (*W.*) *symmetrica*; Downie, Husain & Williams 1971); Middle and ? Upper Eocene of north Germany (Gocht 1969).

Wetzeliella (Wetzeliella) reticulata Williams & Downie 1966b

Pl. 19, fig. 3

1966b *Wetzeliella* (*Wetzeliella*) *reticulata* Williams & Downie: 187; pl. 19, figs 3, 6; text-fig. 48.

DIMENSIONS. Observed range: periphragm 108 × 102 μ to 140 × 144 μ; endophragm 74 × 74 μ to 102 × 108 μ. (n = 5).

REMARKS. In *W.* (*W.*) *reticulata* the processes are mainly arranged in simulate complexes. The processes in each complex are distally united by a complicated network of fine trabeculae, the resulting net being similar in outline and area to the underlying plate area.

OCCURRENCE. Lower Eocene.

PREVIOUS RECORD. Lower Eocene of the London Basin in southern England (Williams & Downie 1966b).

Wetzeliella (Wetzeliella) similis Eisenack 1954

Pl. 19, fig. 4

1954 *Wetzeliella similis* Eisenack : 58 ; pl. 8, figs 8–10.
1966b *Wetzeliella* (*Wetzeliella*) *similis* Eisenack ; Williams & Downie : 194 ; pl. 20, fig. 5.

DIMENSIONS. Observed range : periphragm $78 \times 84\ \mu$ to $116 \times 108\ \mu$; endophragm $54 \times 60\ \mu$ to $72 \times 70\ \mu$. (n = 11).

REMARKS. Specimens here assigned to *W.* (*W.*) *similis* have a broad low apical horn, two distinct lateral horns, a distinct left antapical horn and a much reduced right antapical horn. The endophragm is subcircular in outline, relatively thick walled, and typically granular.

OCCURRENCE. Lower Eocene.

PREVIOUS RECORDS. Lower Eocene of Belgium (De Coninck 1972*) and of the Hampshire and London Basins in southern England (Williams & Downie 1966b) ; Middle and Upper Eocene of north Germany (Agelopoulos 1967) ; Upper Eocene of East Prussia (Eisenack 1954).

Wetzeliella (Wetzeliella) tenuivirgula Williams & Downie 1966b

Pl. 20, figs 1–2

1966b *Wetzeliella* (*Wetzeliella*) *tenuivirgula* Williams & Downie : 188 ; pl. 19, figs 2, 4 ; text-fig. 49.

DIMENSIONS. Observed range : periphragm $72 \times 78\ \mu$ to $164 \times 162\ \mu$; endophragm $54 \times 40\ \mu$ to $122 \times 114\ \mu$. (n = 13).

REMARKS. In *W.* (*W.*) *tenuivirgula* the majority of the processes are arranged in simulate complexes. Adjacent processes in each complex are distally united by thin trabeculae. Additional distal trabeculae may also develop crossing the complexes, and giving the appearance of a loose open net, which, however, never attains the complexity exhibited in *W.* (*W.*) *reticulata*. Specimens here assigned to *W.* (*W.*) *tenuivirgula* show considerable variation in the length of the horns (Pl. 20, figs 1, 2).

OCCURRENCE. Lower and Middle Eocene.

PREVIOUS RECORDS. Lower Eocene of northern France (Chateauneuf & Gruas-Cavagnetto 1968*), of northern Spain (Caro 1973) and of the London Basin in southern England (Williams & Downie 1966b ; Downie, Husain & Williams 1971*).

Wetzeliella (Wetzeliella) tenuivirgula var. ***crassoramosa*** Williams & Downie 1966b

Pl. 20, fig. 3

1966b *Wetzeliella* (*Wetzeliella*) *tenuivirgula* var. *crassoramosa* Williams & Downie : 189 ; pl. 19, figs 1, 5, 7 ; text-fig. 50.

Dimensions. Overall 102 × 108 μ. (n = 1).

Remarks. A single specimen is here attributed to this distinctive variety of *W.* (*W.*) *tenuivirgula*. The processes are distally united by extremely thick trabeculae, but the latter do not attain the appearance of the outer 'shell' developed in *Kisselevia insolens* n. sp. (p. 292).

Occurrence. Lower Eocene.

Previous Records. Lower Eocene of the Hampshire and London Basins in southern England (Williams & Downie 1966b ; Downie, Husain & Williams 1971).

Wetzeliella (Wetzeliella) varielongituda Williams & Downie 1966b

Pl. 20, fig. 4

1966b *Wetzeliella* (*Wetzeliella*) *varielongituda* Williams & Downie : 196 ; pl. 20, figs 4, 8.

Dimensions. Observed range : periphragm 72 × 78 μ to 164 × 162 μ ; endophragm 54 × 40 μ to 122 × 114 μ. (n = 13).

Remarks. *W.* (*W.*) *varielongituda* is characterized by a subtetragonal outline, a broad low apical horn, and reduced lateral and antapical horns. The endophragm is subcircular in outline and thick walled.

Occurrence. Lower, Middle and Upper Eocene.

Previous Records. Lower Eocene of Belgium (De Coninck 1972*), of north Germany (Gocht 1969) and of the Hampshire and London Basins in southern England (Williams & Downie 1966b ; Downie, Husain & Williams 1971*) ; Middle Eocene of north Germany (Gocht 1969) ; Upper Eocene – Lower Oligocene of Russia (Vozzhennikova 1967).

Subgenus ***RHOMBODINIUM*** Gocht 1955

Gocht's (1955) genus *Rhombodinium* was made a subgenus of *Wetzeliella* Eisenack 1938 by Alberti (1961).

Wetzeliella (Rhombodinium) glabra (Cookson) Vozzhennikova 1967

Pl. 20, fig. 5

1956 *Wetzeliella glabra* Cookson : 186 ; pl. 2, figs 1–5.
1967 *Rhombodinium glabra* (Cookson) Vozzhennikova : 169.

Dimensions. Observed range : periphragm 130 × 132 μ to 140 × 150 μ ; endophragm 66 × 66 μ to 74 × 80 μ. (n = 3).

Remarks. The specimens here assigned to *W.* (*R.*) *glabra* are closely comparable to those recorded from the Lower Eocene of southern England by Williams &

Downie (1966b). They differ from the type material (Eocene of South Australia; Cookson 1956) in having a reduced apical horn and only one distinct antapical horn (left). The right antapical horn is represented by a slight bulge in the periphragm. Wilson (1967c) suggested that the European forms may represent a separate species. However, Morgenroth (1966a) illustrated a specimen (pl. 1, fig. 12) which is intermediate between the Australasian and the European forms (Morgenroth 1966a: pl. 1, fig. 11), suggesting that *W.* (*R.*) *glabra* can exhibit a considerable range of morphological variation.

Occurrence. Lower Eocene.

Previous Records. Lower Eocene of Belgium (Morgenroth 1966a) and of the London Basin in southern England (Williams & Downie 1966b); Upper Eocene of New Zealand (Wilson 1967c); Eocene, undifferentiated, of South Australia (Cookson 1956).

UNKNOWN AFFINITIES GROUP

Genus *HETERAULACACYSTA* Drugg & Loeblich 1967

Heteraulacacysta? leptalea n. sp.

Pl. 21, figs 1–2

Derivation of Name. Greek λεπτᾰλέος, fine, delicate, with reference to the overall appearance of this species.

Diagnosis. Cyst body has a smooth or punctate surface, and a subcircular or elliptical outline in polar view. Periphragm wrinkled and folded, forming low simple crests which define the apical and antapical zones, and at least five plate areas in both the pre- and postcingular zones. Cingular zone bordered by two broad membranous crests with undulating distal margins. Circular fenestrations frequently developed in the proximal area of the cingular crests, along with fine elongate fenestrations aligned at right-angles to the margin of the cyst body. Cingular crests reduced across the sulcal zone.

Holotype. B.M.(N.H.) Palaeont. slide V.57766 (8). Sample W56, bed 19c, Bracklesham Beds, Upper Eocene, Whitecliff Bay, Isle of Wight, England.

Dimensions. Holotype: overall (polar view) $106 \times 90\ \mu$; cyst body (polar view) $76 \times 66\ \mu$; height of cingular crests up to $18\ \mu$. Observed range: overall mean diameter (polar view) $71–100\ \mu$; mean diameter of cyst body (polar view) $53–72\ \mu$; height of cingular crests up to $18\ \mu$. ($n = 10$).

Remarks. All the specimens here assigned to *H.*? *leptalea* n. sp. only show a polar view which is comparable to that of *H. campanula* Drugg & Loeblich 1967, the type species of *Heteraulacacysta*. However, as the full reflected tabulation and the mode of archaeopyle formation have not been determined in *H.*? *leptalea*, the generic assignment is tentative. Small perforations in the periphragm, comparable to those present in the proximal area of the cingular crests, frequently give a punctate appearance to the surface of the cyst body. *H.*? *leptalea* differs from

H. campanula Drugg & Loeblich 1967 in having generally poorly developed low sutural crests, a frequently punctate rather than positively ornamented surface to the cyst body, and in exhibiting circular and elongate fenestrations in the cingular crests.

Occurrence. Middle and Upper Eocene.

Genus ***IMPLETOSPHAERIDIUM*** Morgenroth 1966a

There is considerable variation in the overall form of the solid processes in species assigned to this genus (Fig. 24). Basically they are either rod-like and circular or subcircular in cross-section, or consist of erect membranes with variable distal terminations. Apart from the occasional presence of a polygonal opening which is probably an archaeopyle, no definite indications of reflected tabulation have been observed.

Impletosphaeridium cracens n. sp.

Fig. 25E ; Pl. 21, fig. 6

Derivation of Name. Latin, *cracens*, graceful, with reference to the form of the processes.

Diagnosis. Cyst body spherical or subspherical, with a smooth surface. Processes numerous, consisting of erect membranes of variable breadth, strengthened by rod-like thickenings. Processes simple or branched, frequently proximally united by lateral extension of the membranes. Distally the processes have a digitate or aculeate margin.

Holotype. B.M.(N.H.) Palaeont. slide V.57745 (1). Sample W27, bed 9a, Bracklesham Beds, Lower Eocene, Whitecliff Bay, Isle of Wight, England.

Dimensions. Holotype : diameter of cyst body 29 μ ; length of processes up to 12 μ. Observed range : diameter of cyst body 18–30 μ ; length of processes up to 13 μ. (n = 10).

Remarks. The membranous processes with their rod-like thickenings distinguish *I. cracens* n. sp. from all described species of *Impletosphaeridium*. *Cordosphaeridium* ? *minimum* (Morgenroth) Benedek 1972 also has rod-like thickenings in its processes, but the latter are distinctly tubular, and not erect membranes as in *I. cracens*.

Occurrence. Lower, Middle and Upper Eocene.

Impletosphaeridium implicatum Morgenroth 1966a

Fig. 25A ; Pl. 21, fig. 10

1966a *Impletosphaeridium implicatum* Morgenroth : 34 ; pl. 9, figs 1–3.
1968 *Adnatosphaeridium ? capilatum* De Coninck : 39 ; pl. 11, figs 9–13, 21–24 ; not fig. 14.

Description. The subspherical cyst body bears a dense cover of solid processes which are circular or subcircular in cross-section, simple or branched, with long flexuous distal terminations.

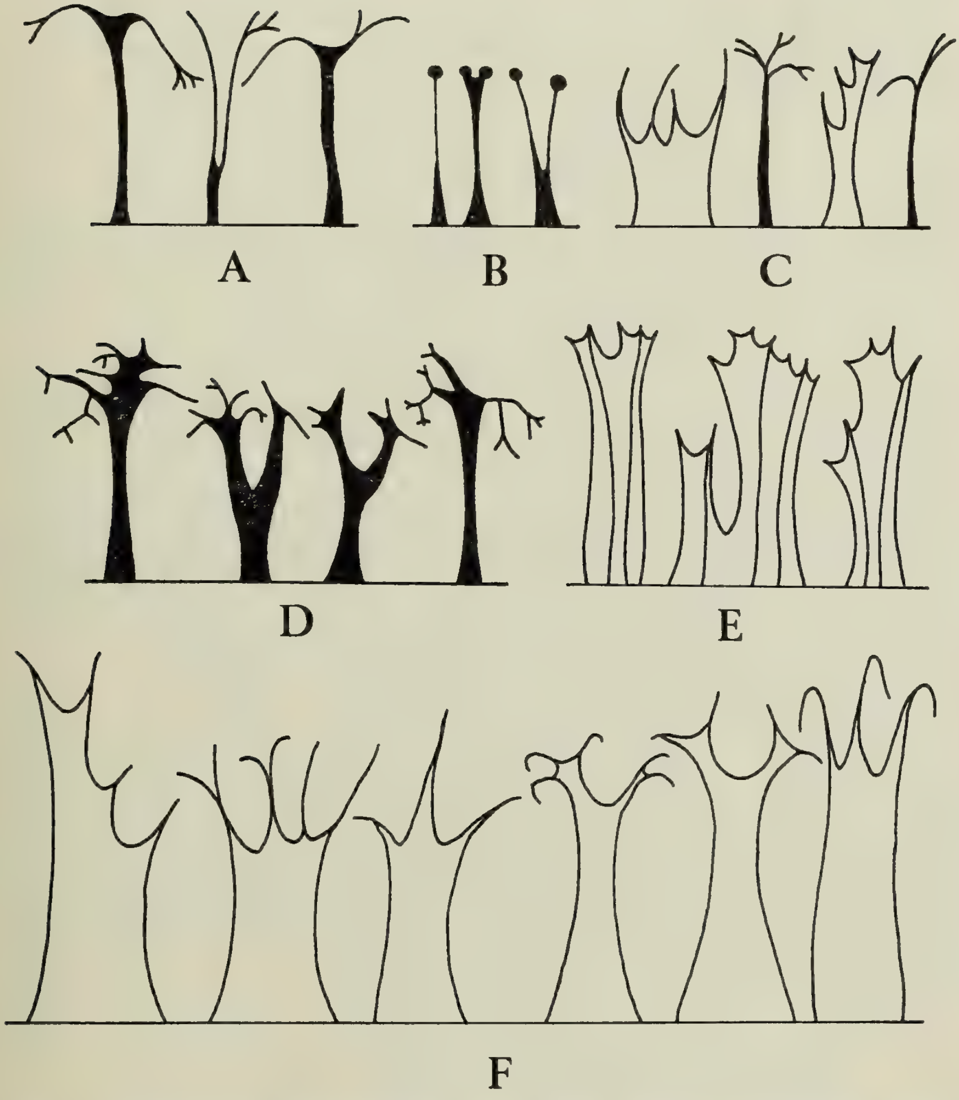


FIG. 25. Diagrammatic representation of process form in *Impletosphaeridium* Morgenroth 1966a. Shaded processes are circular or subcircular in cross-section; unshaded processes are membranous, and 'blade-like' in cross-section. A. *I. implicatum* Morgenroth 1966a. B. *I. insolitum* n. sp. C. *I. kroemmelbeini* Morgenroth 1966a. D. *I. rugosum* Morgenroth 1966a. E. *I. cracens* n. sp. F. *I. luxurium* n. sp.

Dimensions. Observed range: diameter of cyst body 24–39 μ; length of processes up to 13 μ. (n = 3).

Remarks. Most of the specimens assigned to *Adnatosphaeridium* ? *capilatum* by De Coninck (1968) and Gruas-Cavagnetto (1970) possess the flexuous processes characteristic of *I. implicatum*, although one illustrated by De Coninck (1968: pl. 11, fig. 14) has very short, apparently simple processes; this form is not included here.

Occurrence. Lower and Middle Eocene.

Previous Records. Lower Eocene of north Germany (Morgenroth 1966a), of Belgium (De Coninck 1968, as *Adnatosphaeridium* ? *capilatum*) and of northern France (Gruas-Cavagnetto 1970b, as *A.* ? *capilatum*).

Impletosphaeridium insolitum n. sp.

Fig. 25B; Pl. 21, figs 5, 8

Derivation of Name. Latin, *insolitus*, unusual, odd, with reference to the form of the processes.

Diagnosis. Cyst body spherical or subspherical, with a smooth or finely granular surface. Processes numerous, slender and solid. They are simple or bifurcate, with small bulbous spherical or subspherical distal terminations, and may be thickened by the development of proximal membrane; membrane may also be present in the angle of bifurcation.

Holotype. B.M.(N.H.) Palaeont. slide V.57759 (13). Sample W51, bed 17, Bracklesham Beds, Middle Eocene, Whitecliff Bay, Isle of Wight, England.

Dimensions. Holotype: diameter of cyst body 22 μ; length of processes up to 9 μ. Observed range: diameter of cyst body 15–24 μ; length of processes up to 9 μ. (n = 10).

Remarks. Most specimens have simple and bifurcate processes but a few have been observed in which all the processes are simple. The point of bifurcation usually occurs within the distal half of the process. The cyst body occasionally shows a polygonal opening, but no other indications of reflected tabulation have been observed. The unusual form of the processes distinguishes *I. insolitum* n. sp. from all other described species of *Impletosphaeridium*.

Occurrence. Lower, Middle and Upper Eocene.

Impletosphaeridium kroemmelbeini Morgenroth 1966a

Fig. 25C; Pl. 21, fig. 9

1966a *Impletosphaeridium krömmelbeini* Morgenroth: 34; pl. 9, figs 4–5.

Description. Cyst body spherical or subspherical with two types of processes – some slender and rod-like, circular or subcircular in cross-section, and distally bifurcate or multifurcate; others blade-like, membranous, variable in breadth and branched or digitate, with typically aculeate distal terminations.

DIMENSIONS. Observed range: diameter of cyst body 28–35 μ; length of processes up to 15 μ. (n = 5).

OCCURRENCE. Middle and Upper Eocene.

PREVIOUS RECORD. Lower Eocene of north Germany (Morgenroth 1966a).

Impletosphaeridium luxurium n. sp.

Fig. 25F; Pl. 21, figs 3–4

DERIVATION OF NAME. Latin, *luxuria,* excess, with reference to the large number of processes present in this species.

DIAGNOSIS. Cyst body subspherical with a smooth surface. Processes numerous, membranous and of variable breadth. They are bifurcate or digitate with slender aculeate distal terminations.

HOLOTYPE. B.M.(N.H.) Palaeont. slide V.57791 (12). Sample AB40, bed 19, Bracklesham Beds, Upper Eocene, Alum Bay, Isle of Wight, England.

DIMENSIONS. Holotype: diameter of cyst body 37 μ; length of processes up to 15 μ. Observed range: diameter of cyst body 30–37 μ; length of processes up to 16 μ. (n = 6).

REMARKS. The processes in *I. luxurium* n. sp. are similar to the membranous ones in *I. kroemmelbeini* Morgenroth 1966a. *I. luxurium* is usually distinguished, however, by having broader processes, and does not exhibit the slender rod-like ones which are present in *I. kroemmelbeini.*

OCCURRENCE. Middle and Upper Eocene.

Impletosphaeridium rugosum Morgenroth 1966a

Fig. 25D; Pl. 21, fig. 7

1966a *Impletosphaeridium rugosum* Morgenroth: 36; pl. 10, figs 2–3.

DESCRIPTION. Cyst body spherical or subspherical. Processes numerous, solid, and circular or subcircular in cross-section. They are simple or branched and 'tree-like' in overall form, and have slender aculeate distal terminations which may be simple, bifurcate or multifurcate.

DIMENSIONS. Observed range: diameter of cyst body 18–33 μ; length of processes up to 13 μ. (n = 9).

OCCURRENCE. Lower and Middle Eocene.

PREVIOUS RECORD. Lower Eocene of north Germany (Morgenroth 1966a).

IV. THE STRATIGRAPHICAL APPLICATION OF DINOFLAGELLATE CYSTS IN THE BRACKLESHAM BEDS OF THE ISLE OF WIGHT

a. *Microplankton zonation of the Bracklesham Beds*

The distribution of the 106 microplankton taxa recorded from the Bracklesham Beds of Whitecliff Bay is shown in Figs 22 (p. 296) and 26, and of Alum Bay in Figs 27 and 28. A series of five informal microplankton zones is proposed for the Bracklesham Beds of the Isle of Wight based on the stratigraphical ranges of 70 selected species, all but two of which are present in both sections. *Lanternosphaeridium lanosum* and *Wetzeliella* (*W.*) *tenuivirgula* var. *crassoramosa* were only recorded at Alum Bay. The majority of the selected species have not been recorded from the London Clay of the Isle of Wight, and they are considered to have their stratigraphical inception within the Bracklesham Beds. The remaining species which have been recorded from the London Clay at Whitecliff Bay (Williams 1963, Davey *et al.* 1966a) persist into the Bracklesham Beds but not into the overlying Barton Beds (Bujak 1973). The stratigraphical ranges at Whitecliff Bay and Alum Bay of the selected species are shown in Figs 29 and 30 respectively.

There is a fairly regular appearance of stratigraphically new species through the type section of the Bracklesham Beds at Whitecliff Bay (Fig. 29), and hence the selection of zone boundaries based purely on palaeontological data is somewhat arbitrary. For this reason, and because this is the type section, the informal zone boundaries have been deliberately selected to coincide with significant lithological boundaries.

MICROPLANKTON ZONE 1. Whitecliff Bay: bed 1–bed 4 (Fisher beds I–III); Alum Bay: bed 1–bed 2f.

This zone is characterized by the appearance of 15 species which persist into higher zones of the Bracklesham Beds, but have not been recorded from the London Clay of the Isle of Wight: *Achilleodinium biformoides*, *Adnatosphaeridium vittatum*, *Cyclonephelium vicinum*, *Eocladopyxis peniculatum*, *Homotryblium abbreviatum*, *Hystrichokolpoma granulata*, *Impletosphaeridium implicatum*, *I. insolitum*, *I. rugosum*, *Lanternosphaeridium axiale*, *Phthanoperidinium echinatum*, *Polysphaeridium subtile*, *Samlandia chlamydophora*, *Wetzeliella* (*W.*) *coleothrypta* and *W.* (*W.*) *tenuivirgula*.

L. axiale was recorded in this zone at Whitecliff Bay, but at Alum Bay it was not recorded below Zone 2. *S. chlamydophora* and *I. implicatum* were recorded in this zone at Alum Bay, but at Whitecliff Bay the former species was not recorded below Zone 2, and the latter species not below Zone 3.

This zone is further characterized by the rare occurrence of *Kisselevia insolens*, *Lanternosphaeridium lanosum*, *Wetzeliella* (*R.*) *glabra*, *Wetzeliella* (*W.*) *condylos* and *W.* (*W.*) *reticulata*. None of these species has been recorded above Zone 1, or from the London Clay at Whitecliff Bay, although the last three species are known to occur in the London Clay of the London Basin (Williams & Downie 1966b).

Hystrichosphaeridium tubiferum and *Wetzeliella* (*W.*) *similis* are present throughout the London Clay at Whitecliff Bay and both persist into Zone 1 of the Bracklesham Beds. Neither species was recorded in higher zones.

The microplankton assemblages in Zone 1 frequently include numerous examples of the *Areoligera senonensis* complex, forming over 30% of the assemblage at some horizons. Three of the species in this complex (*A. coronata*, *A. medusettiformis* and *A. senonensis*) were not recorded above Zone 1; the other three (*A.* cf. *coronata*, *A.* cf. *medusettiformis* and *A.* cf. *senonensis*) persist into Zone 4, but the complex as a whole does not form a significant proportion of the microplankton assemblages above Zone 1.

The lack of palynological data from the barren Bagshot Sands tends to exaggerate the stratigraphical significance of the appearance of several dinoflagellate cyst

SUCCESSION			TAXA	*Deflandrea depressa*	*D. phosphoritica*	*D. wetzeli*	*Kisselevia insolens*	*Lejeunia hyalina*	*Palaeocystodinium golzowense*	*Phthanoperidinium alectrolophum*	*P. echinatum*	*P. tritonium*	*Wetzeliella (R) glabra*	*Wetzeliella (W.) articulata*	*W. (W.) coleothrypta*	*W. (W.) condylos*	*W. (W.) homomorpha*	*W. (W.) lunaris*	*W. (W.) meckelfeldensis*	*W (W.) reticulata*	*W (W.) similis*	*W. (W.) tenuivirgula*	*W. (W.) varielongituda*			*Heteraulacacysta? leptalea*	*Impletosphaeridium cracens*	*I. implicatum*	*I. insolitum*	*I. kroemmelbeini*	*I. luxurium*	*I. rugosum*
CLAYS	19	c	58		X				X		X			X	X		X									X	X				X	
			57								X			X												X	X		X			
			56		X	X			X		X	X		X	X		X						X			X						
		b	55		X					X				X															X	X		
		a	54									X		X	X																X	
SAND-ROCK	18		53											X																		
SANDY CLAYS	17		52								X				X																	
			51		X	X			X		X			X	X												X		X		X	
SANDS	16		50																													
			49																													
			48																													
SANDS	15		47																													
SANDY CLAYS	14		46		X						X	X		X	X															X		X
SANDS	13		45		X										X																	
SANDY CLAYS	12		44		X	X					X			X	X																	
			43		X									X	X							X										
LAMINATED BEDS	11		42																			X										
			41									X		X			X					X										
			40	X	X	X					X	X		X			X					X	X									
GREENSANDS	10	b	39		X	X		X			X	X		X	X		X					X							X			
			38		X	X						X		X	X		X	X				X	X				X				X	X
		a	37			X								X								X					X			X		
			36			X								X								X					X			X		
			35									X		X													X			X		
			34											X								X					X					X
			33			X								X													X			X		
			32		X	X					X	X		X			X	X								X	X	X		X		X
			31			X						X		X													X					
			30		X	X						X		X			X						X				X			X		
LAMINATED BEDS	9	c	29		X									X			X															
		b	28A		X									X	X		X															
		a	28											X																		
			27		X							X		X			X										X	X				
			26A		X							X		X	X		X		X								X					
LIGNITE & UNDERCLAY	8		26																													
			25B																													
			25A																													
LAMINATED BEDS	7		25		X									X	X		X															X
			24								X						X															X
			23			X					X			X	X		X	X				X										X
GREENSAND	6		22A											X			X															
SANDY CLAYS	5		22			X								X	X		X	X	X										X			X
			21											X																		
			20			X		X			X			X	X		X		X			X							X			X
			19			X					X				X		X															X
			18		X			X			X				X		X	X														X
LAMINATED BEDS	4		17		X	X			X		X				X		X															X
SANDS	3		16																													
LAMINATED BEDS	2		15		X										X		X												X			
			14								X			X	X		X															X
			13		X	X							X	X	X		X	X	X													
			12		X	X								X	X																	X
			11																													
			10																													
			9		X	X					X			X	X		X															X
			8																													
SANDY CLAYS	1		7		X	X								X	X		X															X
			6		X	X	X							X	X	X	X	X	X	X	X	X	X						X			
			5								X			X																		
			4		X	X		X			X			X	X	X	X	X			X								X			
			3			X					X			X							X								X			
			2			X																										
			1																													

FIG. 26. Distribution of dinoflagellate cyst taxa assigned to the Peridiniacean and Unknown Affinities Groups in the Bracklesham Beds at Whitecliff Bay, Isle of Wight.

SUCCESSION			TAXA	*Achilleodinium biformoides*	*Achomosphaera alcicornu*	*A. membraniphora*	*A. ramulifera*	*Adnatosphaeridium multispinosum*	*A. robustum*	*A. vittatum*	*Araneosphaera araneosa*	*Areoligera coronata*	*A. cf. coronata*	*A. medusettiformis*	*A. cf. medusettiformis*	*A. senonensis*	*A. cf. senonensis*	*A. sentosa*	*A. tauloma*	*A. undulata*	*Areosphaeridium arcuatum*	*A. diktyoplokus*	*A. multicornutum*	*Cannosphaeropsis reticulensis*	*Chiropteridium cf. dispersum*	*Cordosphaeridium exilimurum*	*C. fibrospinosum*	*C. gracilis*	*C. inodes*	*C.? minimum*	*C. multispinosum*	*Cyclonephelium divaricatum*	*C. exuberans*
SANDY CLAYS	19		44	X		X	X	X		X	X									X	X	X	X					X	X				
			43				X	X										X		X		X	X			X			X				
			42	X			X	X		X	X							X	X	X		X	X					X	X				
			41			X	X	X			X							X		X		X						X	X				
			40	X		X	X	X			X							X		X		X	X						X	X			X
SANDS	18		39																														
			38																														
CLAYS	17		37																														
CLAYS & LIGNITES	16		36																														
			35																														
			34																														
SANDS	15		33																														
			32																														
			31A																														
			31																														
			30																														
			29																														
LAMINATED BEDS	14	d	28	X		X	X	X			X						X				X	X						X	X				
			27A	X		X	X	X			X										X				X		X	X	X			X	X
		c	27																														
		b	26				X	X		X																	X	X	X			X	
		a	25B				X	X		X																	X	X	X				
CLAY	13		25A																														
			25																														
LAMINATED BEDS	12		24C	X			X	X		X	X													X		X	X	X	X				X
			24B	X	X		X	X																		X		X	X				X
CLAY	11		24A																														
SANDS	10		24																														
			23																														
			22																														
LAMINATED BEDS	9		21				X	X		X								X										X	X				X
			20				X	X											X														
			19	X			X	X		X								X	X										X		X		X
			18	X			X	X							X			X	X			X						X	X				X
			17B				X	X										X	X									X	X			X	X
CLAY	8		17A																														
SANDS	7		17																														
PIPECLAY	6		16																														
SAND & PIPECLAYS	5	b	15																														
		a	14A																														
SANDS	4		14																														
SANDS & PIPECLAYS	3		13																														
LAMINATED BEDS	2	g	12				X	X							X														X		X		X
			11	X			X	X		X			X		X		X							X		X	X	X	X		X	X	X
		f	10				X	X					X		X		X											X					X
		e	9				X	X		X			X		X		X										X	X			X	X	X
		d	8				X	X					X		X		X											X			X	X	X
		c	7				X	X					X		X		X														X	X	
			6				X	X					X		X		X											X			X		
			5		X		X	X	X				X		X		X									X	X	X				X	X
			4A	X			X	X	X	X			X	X	X		X							X		X	X	X	X		X	X	X
			4				X	X	X	X		X	X		X		X							X			X	X			X	X	X
		b	3				X	X																									
		a	2																										X				X
SANDS	1	b	1A				X						X	X	X	X																X	X
		a	1				X		X	X				X	X	X	X									X	X	X	X			X	

Fig. 27. Distribution of dinoflagellate cyst taxa assigned to the Go

C. spinetum	C. vicinum	Diphyes colligerum	Distatodinium craterum	D. ellipticum	D. paradoxum	Eocladopyxis peniculatum	Gonyaulacysta tenuitabulata	Homotryblium abbreviatum	H. oceanicum	H. tenuispinosum	Hystrichokolpoma eisenacki	H. granulata	H. rigaudae	H. salacia	Hystrichosphaeridium asterium	H. patulum	H. pseudorecurvatum	H. tubiferum	Lanternosphaeridium axiale	L. lanosum	L. radiatum	L. vectense	Leptodinium membranigerum	Lingulodinium machaerophorum	Litosphaeridium? inversibuccinum	Membranilarnacia ursulae	Operculodinium centrocarpum	Pentadinium laticinctum	Polysphaeridium subtile	Samlandia chlamydophora	Spiniferites cingulatus	S. monilis	S. pseudofurcatus	S. ramosus var. granomembranaceus	S. ramosus var. granosus	S. ramosus var. membranaceus	S. ramosus var. multibrevis	S. ramosus var. ramosus	Thalassiphora delicata	T. pelagica	Turbiosphaera galatea	T. magnifica
	X	X		X	X		X		X	X			X	X							X	X		X			X	X		X		X	X	X	X	X	X	X	X			
		X							X				X											X			X									X		X				
		X	X	X	X		X	X	X	X			X	X		X					X	X	X	X			X		X	X			X	X	X	X	X	X	X			
	X	X							X	X						X						X	X	X			X								X	X	X	X				
	X	X	X				X		X	X			X	X	X	X	X				X	X	X	X			X	X	X	X		X	X	X	X	X	X	X	X	X		
X	X	X					X	X		X			X			X						X		X			X	X						X	X	X	X	X	X			X
	X	X						X		X														X			X							X	X	X	X	X		X		
	X	X								X									X		X			X			X	X	X						X	X	X	X				
	X																							X			X		X								X	X		X		
X	X	X					X	X		X		X	X											X		X	X	X	X				X		X	X	X			X		
	X	X				X	X			X		X	X											X			X	X							X	X	X	X		X		
X		X								X											X			X			X		X			X		X	X	X	X	X		X		
		X						X		X																	X					X		X	X	X	X	X				
		X								X														X				X	X					X		X	X					
X		X				X		X		X						X								X			X	X				X		X	X	X	X	X				
	X									X		X												X		X	X					X		X	X	X	X	X		X		
		X				X		X		X	X		X														X		X							X	X					
		X				X	X	X		X	X	X	X						X		X		X	X			X		X	X			X	X	X	X	X	X		X	X	
		X				X		X		X														X			X							X		X	X	X				
		X					X	X		X		X				X								X	X		X						X	X	X	X	X	X				
		X					X	X		X													X				X								X		X					
		X						X		X																			X					X		X	X	X				
	X	X				X	X	X		X																	X		X							X	X	X				
X		X				X	X	X		X								X		X	X			X		X	X		X			X			X	X	X	X	X	X		
		X				X	X	X		X	X	X				X		X		X	X			X	X		X		X		X		X	X		X	X	X		X		
		X					X	X		X								X			X			X			X		X					X	X	X	X	X		X		
		X				X	X									X								X			X		X							X	X					
		X					X	X																X			X			X							X	X				
		X					X	X													X			X													X	X				
	X	X				X	X					X	X					X			X			X			X		X					X	X		X	X	X			

ac: ean Group in the Bracklesham Beds at Alum Bay, Isle of Wight.

species in the lowest Bracklesham Beds which have not been recorded from the London Clay. If microplankton assemblages from sediments equivalent in age to the Bagshot Sands of the Isle of Wight exist, it is highly likely they will be found to include some of the species which appear in microplankton Zone 1 of the Bracklesham Beds.

MICROPLANKTON ZONE 2. Whitecliff Bay: bed 5–bed 8 (Fisher beds IV–V, in part); Alum Bay: bed 2g. (Although bed 8 (lignite and underclay) at Whitecliff Bay did not yield microplankton, for convenience it is assigned to Zone 2).

This zone is characterized by the appearance of six species which persist into higher zones of the Bracklesham Beds, but were not recorded in Zone 1: *Areosphaeridium diktyoplokus*, *Cyclonephelium laciniiforme*, *C. spinetum*, *Hystrichokolpoma salacia*, *Pentadinium laticinctum* and *Turbiosphaera galatea*.

A single specimen of *Wetzeliella* (*W.*) *tenuivirgula* var. *crassoramosa* is here recorded from Zone 2 at Alum Bay. This form was recorded from the London Clay at Whitecliff Bay (Williams & Downie 1966b), but was not encountered in Zone 1 of the Bracklesham Beds.

The highest records of *Adnatosphaeridium robustum* and *Cyclonephelium* aff. *exuberans* were noted in Zone 2.

At Alum Bay the upper part of Zone 2 and the lower part of Zone 3 are represented by a palynologically barren interval, bed 3 to bed 8. The only interval positively assignable to Zone 2 is bed 2g which has yielded *C. laciniiforme*, *C. spinetum* and *T. galatea*. *A. diktyoplokus* and *P. laticinctum* first appear in bed 9, the lowest interval positively assignable to Zone 3, and *H. salacia* was not recorded below Zone 5.

MICROPLANKTON ZONE 3. Whitecliff Bay: bed 9a–bed 10a (Fisher beds V, in part, –VI); Alum Bay: bed 9–bed 14c.

This zone is characterized by the appearance of 10 species which persist into higher zones of the Bracklesham Beds, but were not recorded below Zone 3: *Araneosphaera araneosa*, *Areoligera sentosa*, *A. tauloma*, *Chiropteridium* cf. *dispersum*, *Cordosphaeridium* ? *minimum*, *Heteraulacacysta* ? *leptalea*, *Impletosphaeridium cracens*, *I. kroemmelbeini*, *I. luxurium* and *Phthanoperidinium tritonium*.

C. cf. *dispersum*, *H.* ? *leptalea* and *C.* ? *minimum* were recorded in this zone at Whitecliff Bay, but at Alum Bay the first two species were not recorded below Zone 4, and the third species not below Zone 5. *I. luxurium* was recorded in this zone at Alum Bay, but at Whitecliff Bay it was not recorded below Zone 4.

The highest records of *Hystrichokolpoma granulata*, *Turbiosphaera galatea* and *Wetzeliella* (*W.*) *meckelfeldensis* were noted in Zone 3.

As mentioned above, the lower part of Zone 3 at Alum Bay is represented by palynologically barren sediments.

MICROPLANKTON ZONE 4. Whitecliff Bay: bed 10b–bed 18 (Fisher beds VII–XVI); Alum Bay: bed 14d–e.

This zone is characterized by the appearance of four species which persist into Zone 5 of the Bracklesham Beds, but were not recorded below Zone 4: *Achomosphaera membraniphora*, *Areosphaeridium arcuatum*, *Homotryblium oceanicum* and

SUCCESSION			TAXA	Deflandrea phosphoritica	D. wetzeli	Kisselevia insolens	Lejeunia hyalina	Palaeocystodinium golzowense	Phthanoperidinium alectrolophum	P. echinatum	P. tritonium	Wetzeliella (R.) glabra	Wetzeliella (W.) articulata	W. (W.) coleothrypta	W. (W.) condylos	W. (W.) homomorpha	W. (W.) lunaris	W. (W.) meckelfeldensis	W. (W.) reticulata	W. (W.) similis	W. (W.) tenuivirgula	W. (W.) tenuivirgula var. crassoramosa	W. (W.) varielongituda			Heteraulacacysta? leptalea	Impletosphaeridium cracens	I. implicatum	I. insolitum	I. kroemmelbeini	I. luxurium	I. rugosum
SANDY CLAYS	19		44	X				X	X	X	X		X	X												X			X			
			43										X																		X	
			42	X					X	X	X		X	X												X	X		X	X	X	
			41								X		X	X																	X	
			40	X					X	X	X		X	X												X	X				X	
SANDS	18		39																													
			38																													
CLAYS	17		37																													
CLAYS & LIGNITES	16		36																													
			35																													
			34																													
SANDS	15		33																													
			32																													
			31A																													
			31																													
			30																													
			29																													
LAMINATED BEDS	14	d	28	X									X	X							X					X		X				X
			27A										X	X							X							X				
		c	27																													
		b	26	X									X	X																		
		a	25B	X									X	X		X					X											
CLAY	13		25A																													
			25																													
LAMINATED BEDS	12		24C	X									X			X					X									X		
			24B	X	X						X		X			X					X							X				
CLAY	11		24A																													
SANDS	10		24																													
			23																													
			22																													
LAMINATED BEDS	9		21	X							X		X			X											X				X	
			20								X		X														X			X		
			19								X		X																			
			18	X	X						X		X																	X		
			17B	X						X	X		X														X					
CLAY	8		17A																													
SANDS	7		17																													
PIPECLAY	6		16																													
SAND & PIPECLAYS	5	b	15																													
		a	14A																													
SANDS	4		14																													
SANDS & PIPECLAYS	3		13																													
LAMINATED BEDS	2	g	12							X				X		X												X				
			11	X									X	X		X		X				X										
		f	10											X		X												X				
		e	9		X					X				X		X													X			X
		d	8	X						X			X	X														X				
		c	7										X			X																
			6	X									X			X																
			5	X								X	X	X						X			X						X			
			4A	X		X	X						X	X	X				X	X	X		X									
			4	X	X	X							X	X			X			X	X		X					X				
		b	3							X						X			X										X			X
		a	2							X			X			X																
SANDS	1	b	1A										X			X																
		a	1	X	X					X			X			X	X			X												

FIG. 28. Distribution of dinoflagellate cyst taxa assigned to the Peridiniacean and Unknown Affinities Groups in the Bracklesham Beds at Alum Bay, Isle of Wight.

Lanternosphaeridium vectense. *H. oceanicum* was recorded in this zone at Whitecliff Bay but at Alum Bay it was not recorded below Zone 5.

Turbiosphaera magnifica was found to be restricted to Zone 4 at Whitecliff Bay and Alum Bay although it was recorded from the Barton Beds at Alum Bay by Bujak (1973).

The highest records of the *Areoligera senonensis* complex, *Chiropteridium* cf. *dispersum*, *Cordosphaeridium fibrospinosum*, *Cyclonephelium divaricatum*, *C. ordinatum*, *Eocladopyxis peniculatum*, *Impletosphaeridium implicatum*, *Membranilarnacia ursulae*, *Wetzeliella* (*W.*) *lunaris* and *W.* (*W.*) *tenuivirgula* were noted in Zone 4.

At Alum Bay the upper part of Zone 4 and possibly the lowest part of Zone 5 are represented by an interval which is devoid of microplankton, bed 15 to bed 18. The only interval positively assignable to Zone 4 is bed 14d–e, which has yielded three of the four characteristic species appearing in this zone.

MICROPLANKTON ZONE 5. Whitecliff Bay: bed 19a–c (Fisher beds XVII–XIX, in part); Alum Bay: bed 19.

This zone is characterized by the appearance of eight species which persist into the overlying Barton Beds (Bujak 1973), but were not recorded below Zone 5: *Areoligera undulata*, *Areosphaeridium multicornutum*, *Cyclonephelium intricatum*, *Distatodinium craterum*, *D. ellipticum*, *D. paradoxum*, *Hystrichosphaeridium asterium* and *Phthanoperidinium alectrolophum*.

The highest records of *Achomosphaera membraniphora*, *Adnatosphaeridium vittatum*, *Areoligera sentosa*, *Cordosphaeridium exilimurum*, *Cyclonephelium exuberans*, *C. laciniiforme*, *C. spinetum*, *C. vicinum*, *Hystrichokolpoma salacia*, *Hystrichosphaeridium patulum*, *Impletosphaeridium cracens*, *I. luxurium*, *Lanternosphaeridium vectense* and *Wetzeliella* (*W.*) *varielongituda* were noted in Zone 5. None of these species was recorded from the Barton Beds (Bujak 1973).

The Bracklesham Beds represent the upper part of the Lower Eocene, the Middle Eocene and the lower part of the Upper Eocene (Curry *et al.* 1969). Although none of the proposed microplankton zone boundaries corresponds exactly with the major stratigraphical boundaries suggested by Curry *et al.* (1969), broadly speaking the upper part of the Lower Eocene is represented by microplankton Zones 1 and 2, the Middle Eocene by Zones 3 and 4, and the lower part of the Upper Eocene by Zone 5 (Fig. 29).

This zonal scheme is essentially for local application, but the major palynostratigraphical trends shown by the microplankton assemblages should be recognizable over a much wider geographical area.

b. *Correlation of the Bracklesham Beds at Whitecliff Bay and Alum Bay*

The Bracklesham Beds at Whitecliff Bay and Alum Bay have never been satisfactorily correlated because of the considerable contrast in lithological sequence between the two and the absence of marine faunas at Alum Bay from all but the highest part of the sequence (Eaton 1971b: text-fig. 1). The record of microplankton assemblages through most of the Bracklesham Beds at Whitecliff Bay and in four intervals in the sequence at Alum Bay allows the two sections to be correlated.

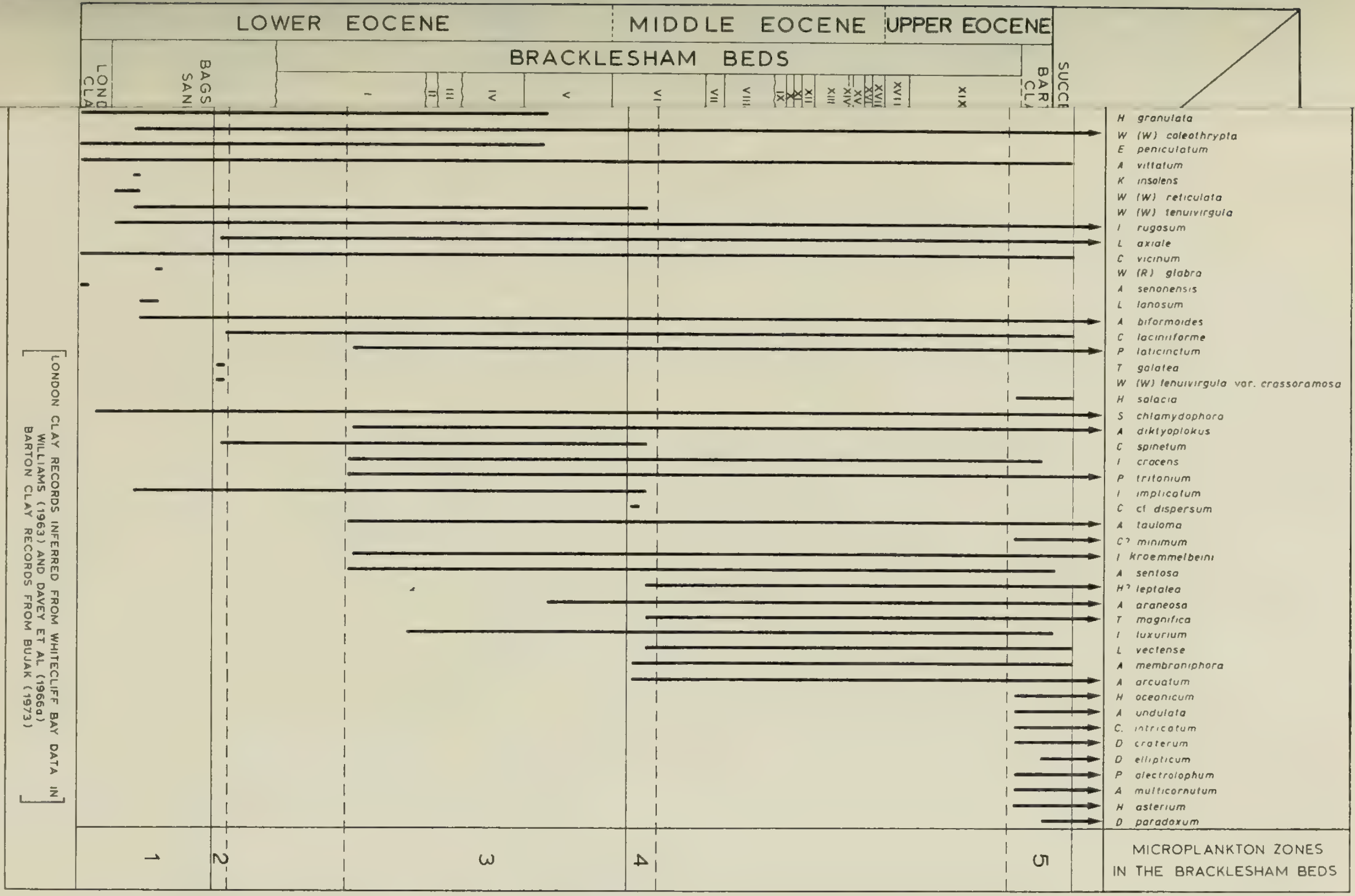


FIG. 30. Stratigraphical ranges of selected dinoflagellate cyst taxa in the Bracklesham Beds at Alum Bay, Isle of Wight.

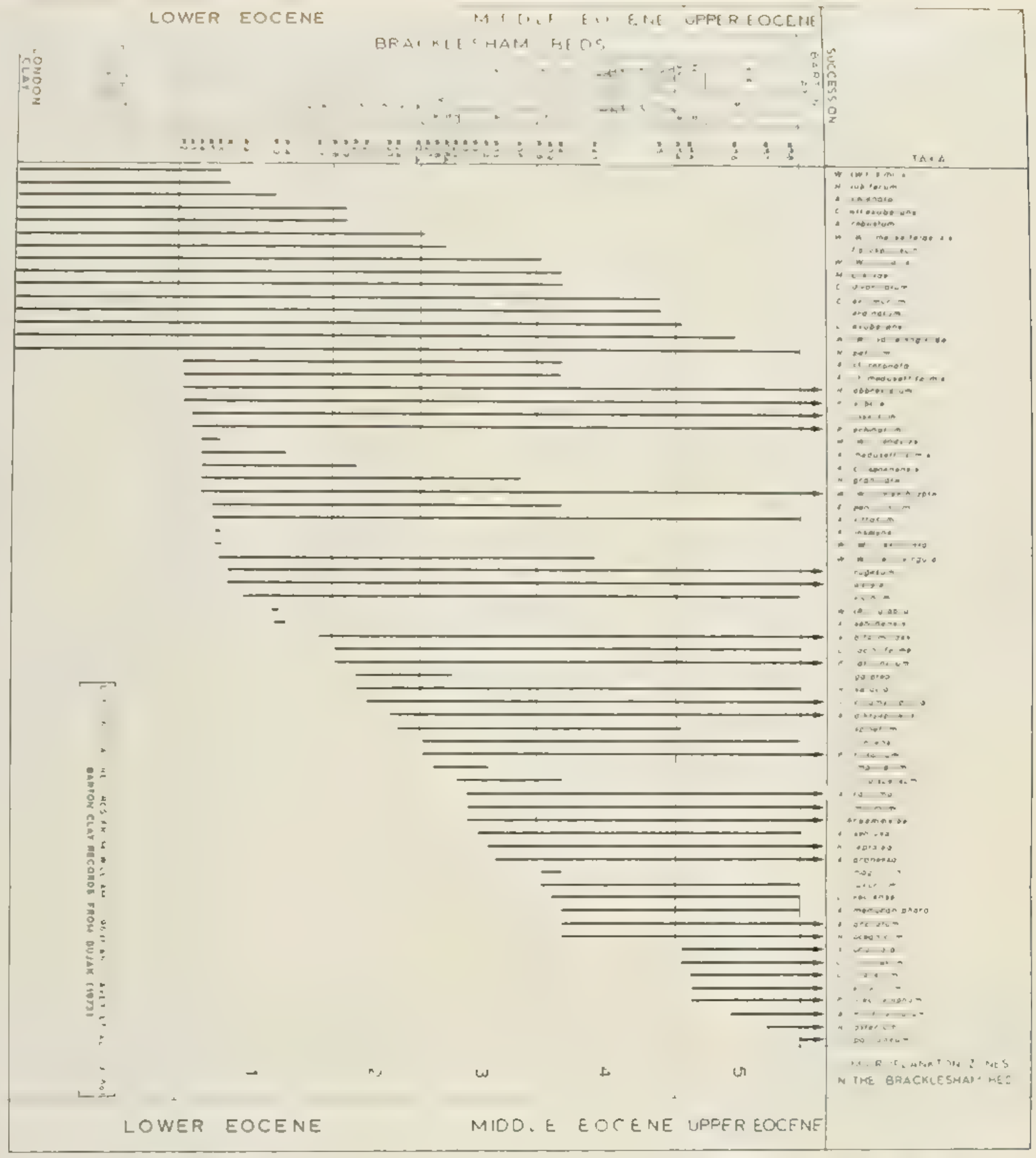


FIG. 29. Stratigraphical ranges of selected dinoflagellate cyst taxa in the Bracklesham Beds at Whitecliff Bay, Isle of Wight

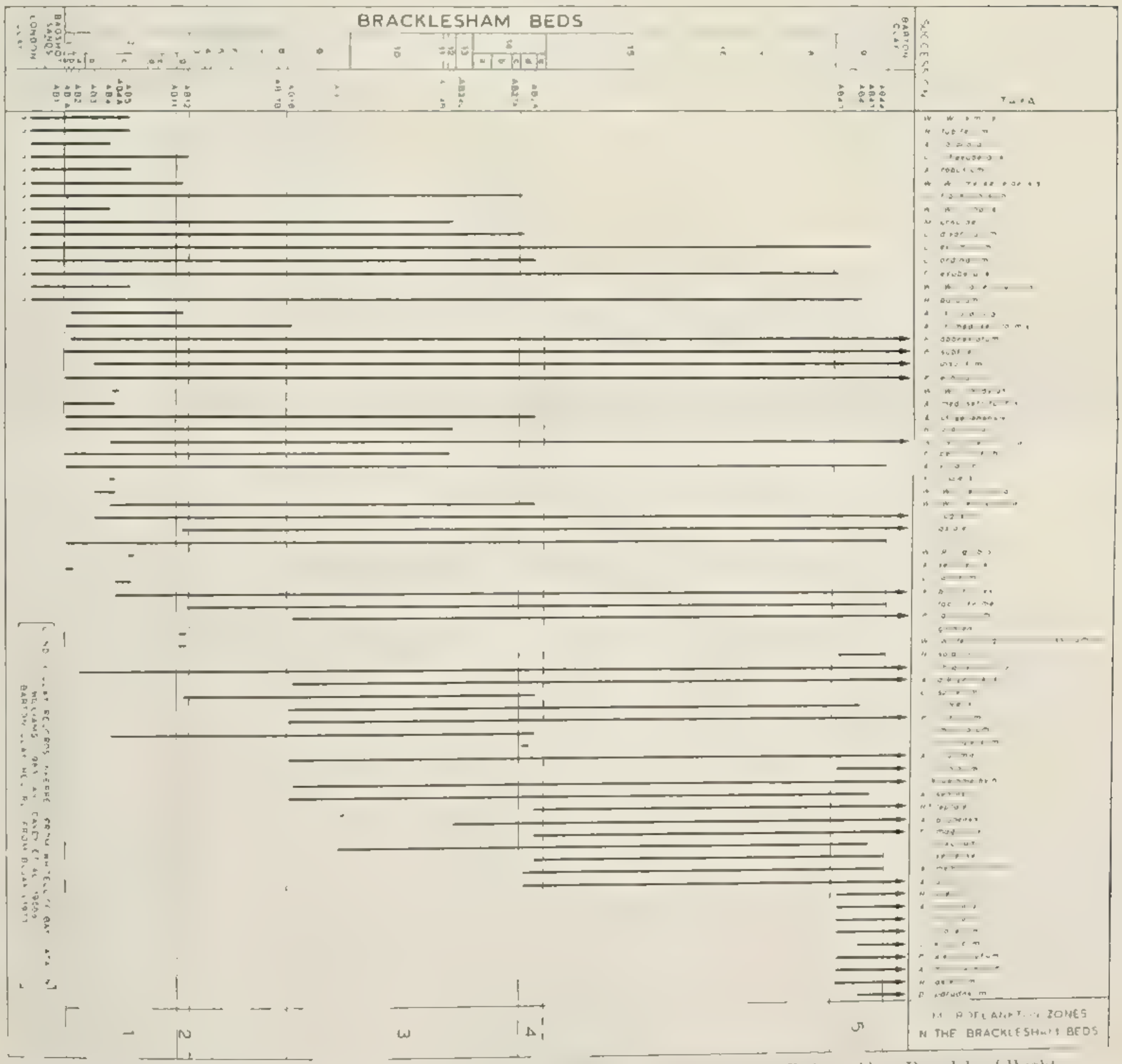


FIG. 30. Stratigraphical ranges of selected dinoflagellate cyst taxa in the Bracklesham Beds at Alum Bay, Isle of Wight

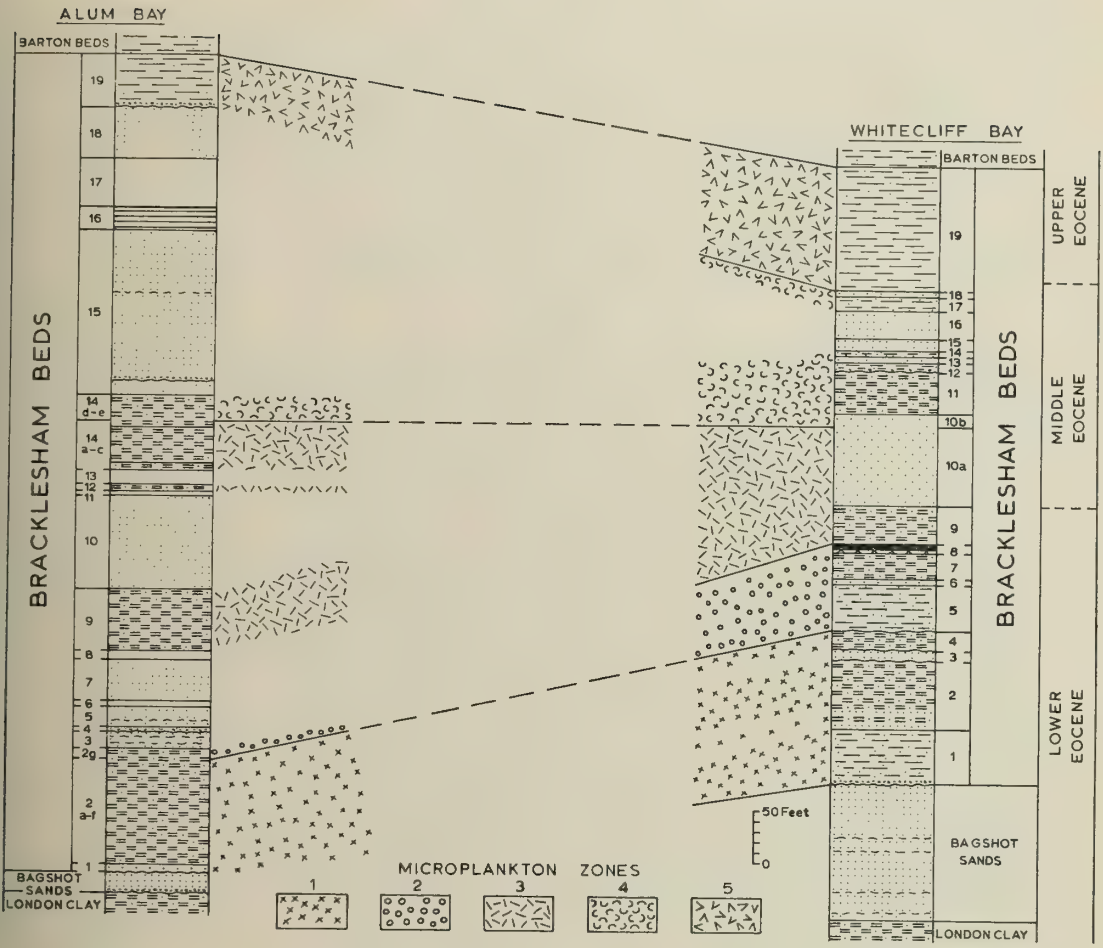

ALUM BAY
BARTON BEDS
BRACKLESHAM BEDS
19
18
17
16
15
14 d-e
14 a-c
13
12
11
10
9
8
7
6
5
4
3
2g
2 a-f
1
BAGSHOT SANDS
LONDON CLAY
WHITECLIFF BAY
BARTON BEDS
19
18
17
16
15
14
13
12
11
10b
10a
9
8
7
6
5
4
3
2
1
BAGSHOT SANDS
LONDON CLAY
UPPER EOCENE
MIDDLE EOCENE
LOWER EOCENE
50 Feet
0
MICROPLANKTON ZONES
1
2
3
4
5

FIG. 31. Comparative distribution of the five microplankton zones in the Bracklesham Beds at Whitecliff Bay and Alum Bay, Isle of Wight.

The comparative distribution of the five microplankton zones in the two sections is shown in Fig. 31. The diagram in Eaton (1971a: text-fig. 2; 1971b: text-fig. 1) indicates that all four interzonal boundaries defined at Whitecliff Bay are recognizable at Alum Bay. Using purely palynological data only the 1/2 and 3/4 zone boundaries can be recognized. Strictly speaking the horizon marking the 4/5 zone boundary cannot be defined at Alum Bay, but using all available geological data there are strong indications that the horizon representing the 2/3 zone boundary at Whitecliff Bay does correlate with the boundary between beds 3 and 4 at Alum Bay.

The sequence of sands and pipeclays (bed 3–bed 8) previously assigned to the Bagshot Sands at Alum Bay (White 1921) are correlated with the upper part of Zone 2 and the lower part of Zone 3 of the Bracklesham Beds at Whitecliff Bay (the sediments associated with the lignite bed, bed 8). The underlying laminated beds and sands at Alum Bay (bed 1a–bed 2g), which have been previously assigned to the London Clay (White 1921), are correlated with Zone 1 and the lower part of Zone 2 of the Bracklesham Beds at Whitecliff Bay. This possibility was suggested by Curry (in Wright & Curry 1959 : 14).

c. *Comparison with microplankton assemblages from the Lower Eocene of the London Basin*

On the north Kent coast in south-east England the Bracklesham Beds are not represented, and the Lower Eocene London Clay is succeeded only by the Bagshot Sands. Microplankton have been described from the London Clay of this area by Williams (1963) and Husain (1967), and the results of their work have been published in Davey *et al.* (1966a) and Downie, Husain & Williams (1971).

Several dinoflagellate cysts which appear in the lowest Bracklesham Beds (microplankton Zone 1) of the Isle of Wight have been noted in the London Clay of north Kent. *Wetzeliella* (*W.*) *tenuivirgula* persists throughout the London Clay in this area, *Eocladopyxis peniculatum, Impletosphaeridium implicatum, I. rugosum* and ? *Phthanoperidinium echinatum* are present in the lower part of the London Clay, and *Polysphaeridium subtile, Wetzeliella* (*R.*) *glabra, Wetzeliella* (*W.*) *condylos* and *W.* (*W.*) *reticulata* are present in the upper part of the London Clay. Although these records do not indicate a simple, straightforward stratigraphical relationship between the microplankton assemblages from the Lower Eocene of the Hampshire and London Basins, the restricted distribution of *P. subtile, W.* (*R.*) *glabra, W.* (*W.*) *condylos* and *W.* (*W.*) *reticulata* suggests that the upper part of the London Clay in north Kent may be younger than the London Clay of the Isle of Wight.

Although microplankton have proved effective for correlating the Bracklesham Beds of the Isle of Wight, considerably more palynological data are required from the northern part of the Hampshire Basin and the western part of the London Basin before the Lower Eocene sediments in southern England can be precisely correlated using microplankton assemblages.

V. COMPARISONS WITH PREVIOUS STUDIES OF EOCENE MICROPLANKTON IN NORTHERN EUROPE

In this section emphasis is placed on studies of Eocene microplankton which have yielded taxa considered to be stratigraphically significant in the Bracklesham Beds of the Isle of Wight.

a. *Belgium*

De Coninck (1968, 1972) described microplankton assemblages from Lower Eocene sediments in a borehole at Kallo near Antwerp. This penetrated (in descending order) Belgian representatives of the Cuisian Argile de Merelbeke (Paniselian) and Sables de Mons-en-Pévèle, and the Sparnacian (in the sense of Curry *et al.* (1969)) Argile d'Ypres.

The stratigraphical appearance of *Homotryblium abbreviatum* (as *Hystrichosphaeridium tubiferum brevispinum*), *Samlandia chlamydophora* and possibly *Achilleodinium biformoides* (as *Hystrichokolpoma ? biformoides*) in the highest 25 metres of the Argile d'Ypres, and of *Areosphaeridium diktyoplokus* in the Argile de Merelbeke, parallels the distribution of these species in microplankton Zones 1 and 2 of the Bracklesham Beds. The possibility of the highest part of the Argile d'Ypres at Kallo being younger than the London Clay of southern England is also indicated by a comparison of the microplankton associations from the two areas (Downie, Husain & Williams 1971 : 34).

Isolated assemblages from the Argile d'Ypres at Langemark, Kortemark and St Jan have been studied by Morgenroth (1966a) and yielded *Achilleodinium biformoides*, *Lanternosphaeridium lanosum*, *Samlandia chlamydophora* and *Wetzeliella* (*R.*) *glabra*. The presence of these species suggests a comparison with the highest part of the Argile d'Ypres at Kallo, and microplankton Zone 1 of the Bracklesham Beds.

b. *North Germany*

There are five divisions in the German Eocene : Lower Eocene 1–4, and Upper Eocene. Lower Eocene divisions 1–3 are considered to be equivalent to the Lower Eocene of the Anglo–Paris–Belgian Basin, and the Middle Eocene is represented by the German Lower Eocene 4.

For comparison with the microplankton assemblages from the Bracklesham Beds, the most significant work on the German Eocene is that of Morgenroth (1966a). He described assemblages from the Tarras (the 'equivalent' of the London Clay in north Germany) on Fehmarn Island. The Tarras has been variously assigned to Lower Eocene 4, Lower Eocene 3/4, and Lower Eocene 2. The rich microplankton assemblages from this lithostratigraphical unit include *Achilleodinium biformoides*, *Adnatosphaeridium robustum*, *Areosphaeridium diktyoplokus*, *Cordosphaeridium ? minimum*, *Eocladopyxis peniculatum*, *Impletosphaeridium implicatum*, *I. kroemmelbeini*, *I. rugosum*, *Lanternosphaeridium axiale*, *L. lanosum* and *Samlandia chlamydophora*.

C. ? minimum and *I. kroemmelbeini* were not recorded below microplankton Zone 3 in the Bracklesham Beds. The specimen of *A. diktyoplokus* figured by Morgenroth (1966a : pl. 4, figs 11–12) is comparable to the earliest representatives of this species recorded in Zones 2 and 3 (Eaton 1971a : pl. 1, fig. 3). *A. robustum* was only recorded in Zones 1 and 2, and *L. lanosum* only in Zone 1 of the Bracklesham Beds. The other six significant species first appear in Zone 1 and persist through Zones 2 and 3.

Although several key species are absent, direct comparison between the north German assemblages and those from the Bracklesham Beds suggests that the Tarras includes representatives of microplankton Zones 1, 2 and 3, i.e. the upper part of the Lower Eocene and possibly the lowest part of the Middle Eocene.

Agelopoulos (1967) described assemblages from Middle and Upper Eocene sediments at Heiligenhafen, north Germany. The Middle Eocene assemblages include

Areosphaeridium diktyoplokus, and this species was also recorded in the Upper Eocene together with *Achilleodinium biformoides*, *Achomosphaera membraniphora* and *Samlandia chlamydophora*. In the Bracklesham Beds these species were recorded in the Upper, Middle and (*A. membraniphora* apart) Lower Eocene.

Gocht (1969) described assemblages from Palaeocene, Lower, Middle and ? Upper Eocene, and Middle Oligocene sediments in two boreholes at Meckelfeld near Hamburg, north Germany. The majority of the assemblages are dominated by *Cordosphaeridium* (*C. inodes* and *C. gracilis*), allowing little comparison with the assemblages from the Bracklesham Beds. It is significant, however, that Gocht noted the persistence of the *Areoligera senonensis* complex into the Middle Eocene, as is the case in the Bracklesham Beds.

c. *Northern France*

Microplankton assemblages recorded from the Eocene of northern France include only a few of the species which are considered to be stratigraphically important in the Bracklesham Beds. The most significant assemblages are those described from the Lower Eocene (Cuisian) Varengeville Formation in Normandy by Gruas-Cavagnetto (1970b). The *Areoligera senonensis* complex forms a prominent part of the assemblages, in association with *Hystrichosphaeridium tubiferum* and *Impletosphaeridium implicatum* (as *Adnatosphaeridium* ? *capilatum*). This suggests a comparison with microplankton Zone 1 of the Bracklesham Beds.

VI. PALYNOSTRATIGRAPHICAL SUMMARY

The potential stratigraphical value of microplankton for correlation in the Eocene of southern England and northern Europe has been demonstrated in sections IV and V of this paper. The most significant palynostratigraphical features of the assemblages encountered in the present study are listed here.

1. The appearance of the genera *Achilleodinium*, *Pentadinium*, *Samlandia* and *Turbiosphaera* in the upper part of the Lower Eocene, *Araneosphaera* in the Middle Eocene, and the appearance and diversification at specific level of *Distatodinium* in the lower part of the Upper Eocene.
2. The diversification at specific level of *Phthanoperidinium* through the Eocene.
3. The appearance of *Areosphaeridium* in the upper part of the Lower Eocene, and its diversification at specific level through the Middle and Upper Eocene.
4. The decline of the *Areoligera senonensis* complex in the Middle Eocene, and its stratigraphical 'replacement' by species with more membranous processes (*A. sentosa*, *A. tauloma*, *A. undulata*).

The microplankton assemblages which have been described from Palaeogene sediments in Europe and other parts of the world frequently only include the more common stratigraphically long-ranging taxa, or they are dominated by forms of apparently restricted geographical distribution. Fortunately, as indicated below, there are records of the morphologically more distinctive taxa considered to be stratigraphically significant in this study, in assemblages other than those discussed in section V.

The most notable of these taxa is *Areosphaeridium*. *A. diktyoplokus* has been recorded from the Tertiary of Europe (Belgium, England, north Germany, Norwegian North Sea, East Prussia, Romania), North America (Aleutian Islands), South America (Argentina including Tierra del Fuego, Chile) and Antarctica. Some of these records are from undifferentiated Tertiary sediments, but there are indications of a stratigraphical range from Lower Eocene to Miocene with particular emphasis on the Eocene.

The only area in which Palaeogene microplankton have been studied in some detail without yielding *A. diktyoplokus* is Australasia, although it has been recorded as a reworked form in the Pleistocene of New Zealand (Wilson 1973). This apparent absence is all the more surprising when it is considered that forms probably referable to *Areosphaeridium* have been recorded from the Upper Eocene of Victoria, Australia – as *Cordosphaeridium capricornum* Cookson & Eisenack 1965 (Eaton 1971a : 364).

Areosphaeridium arcuatum and *A. multicornutum* have only been recorded from the Middle and Upper Eocene and from the Upper Eocene, respectively, of southern England, but other records of forms probably attributable to *Areosphaeridium* include *Baltisphaeridium pectiniforme* from the Middle Oligocene (Gerlach 1961 ; Benedek 1972, as *Cleistosphaeridium pectiniforme*) and Upper Oligocene (Brosius 1963) of north Germany, and '*Baltisphaeridium*' cf. *B. pectiniforme* from the Upper Eocene of the Aleutian Islands, north Pacific Ocean (Evitt 1970). The inception of *Areosphaeridium* in the Eocene and its diversification at specific level through the Eocene and Oligocene appear to be a world-wide feature of Palaeogene microplankton assemblages.

Three species of *Phthanoperidinium* were recorded from the Bracklesham Beds (*P. alectrolophum*, *P. echinatum*, *P. tritonium*). Representatives of this genus are also known from the Palaeocene and the Lower Eocene of northern France (Chateauneuf & Gruas-Cavagnetto 1968, *P. resistente*), the Lower Eocene of north Germany (Morgenroth 1966a, *P. resistente*) and northern Spain (Caro 1973, *P. campoense*), and the Upper Eocene of Victoria, Australia (Cookson & Eisenack 1965, *P. eocenicum*). The persistence of *Phthanoperidinium* into the Oligocene is indicated by records from the Lower Oligocene of north Germany (Morgenroth 1966b, *P. comatum*) and the Oligocene of Mississippi, U.S.A. (Drugg & Loeblich 1967, *P. amoenum*).

Distatodinium is represented by three species in the Upper Eocene part of the Bracklesham Beds (*D. craterum*, *D. ellipticum*, *D. paradoxum*), but published records suggest that this genus is more characteristic of the Oligocene, particularly in Europe. *D. craterum* has been recorded from the Middle Oligocene of Switzerland (Scherer 1961, as *Hystrichosphaeridea*), *D. ellipticum* and *D. tenerum* from the Middle and Upper Oligocene of north Germany (Benedek 1972), and *D. paradoxum* from the Middle Oligocene (Gocht 1969, Benedek 1972) and Upper Oligocene (Brosius 1963, Benedek 1972) of north Germany. *D. ellipticum* is also known from the Upper Eocene of Victoria, Australia (Cookson 1965).

The trend towards marginate cyst taxa with more membranous processes, indicated by the stratigraphical 'replacement' of the *Areoligera senonensis* complex by *Areoligera sentosa*, *A. tauloma* and *A. undulata* through the Middle Eocene, is emphasized by the appearance of *Chiropteridium* cf. *dispersum*, *Cyclonephelium laciniiforme* and *C. spinetum* in the upper part of the Lower Eocene and the Middle Eocene.

A. undulata, which was found to be very common in the Upper Eocene in this study, has also been recorded by Eisenack (1954, as *Palmnickia* sp. indet.) from the Bernstein Formation in the Samland area of East Prussia (now Russia). This formation was then considered to represent the Lower Oligocene, but Eisenack later (1965) assigned it to the Upper Eocene. The persistence and diversification of membranous-processed marginate cyst taxa into the Oligocene are confirmed in microplankton studies of material from north Germany: e.g. Gerlach (1961), Brosius (1963), Gocht (1969) and Benedek (1972).

These records of morphologically distinctive, stratigraphically significant taxa from sediments in widely separated parts of the world hold out considerable hope for the application of microplankton to long range stratigraphical correlation in the Palaeogene.

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PLATE 1

Achilleodinium biformoides (Eisenack 1954) n. comb., emend. (p. 234)

FIG. 1. Upper (ventral) surface of specimen. V.57759 (12) ; W51. × 500.

FIG. 2. Same specimen, mid-focus, × 500.

FIG. 3. Lower (dorsal) surface of same specimen showing precingular archaeopyle. × 500.

FIG. 4. Specimen showing development of proximal fenestrations in the postcingular processes. V.57757 (8) ; W40. × 500.

FIG. 5. Lower (ventral) surface of specimen. V.57754 (1) ; W38. × 500.

FIG. 6. Specimen V.57750 (7) ; W32. × 500.

Achomosphaera ramulifera (Deflandre) Evitt 1963 (p. 236)

FIG. 7. Specimen V.57768 (1) ; W57. × 500.

Achomosphaera membraniphora (Agelopoulos 1964) n. comb., emend. (p. 237)

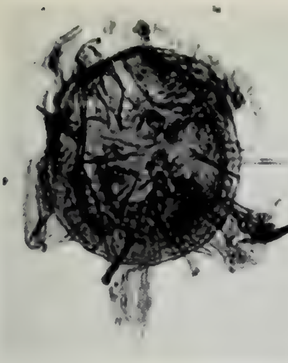
FIG. 8. Specimen showing precingular archaeopyle, and pericoel developed over the ventral area of the hypotract. V.57797 (3) ; AB40. × 500.

FIG. 9. Specimen clearly showing the pericoel developed over the ventral surface. V.57764 (5) ; W56. × 500.

FIG. 10. Specimen showing precingular archaeopyle. V.57766 (13) ; W56. × 500.

Achomosphaera alcicornu (Eisenack) Davey & Williams 1966a (p. 236)

FIG. 11. Specimen V.57757 (2) ; W40. × 500.



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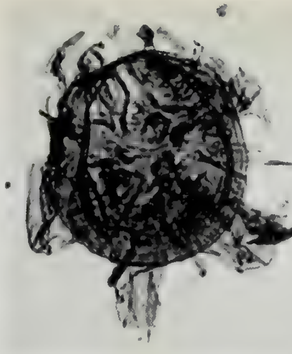

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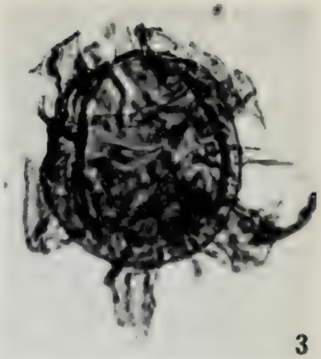

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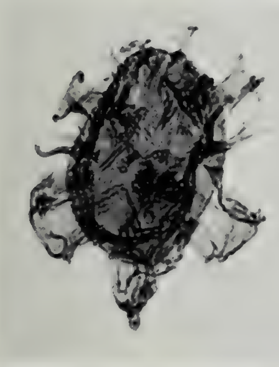

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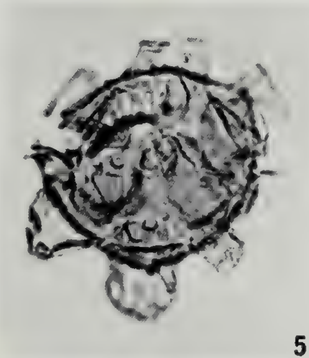

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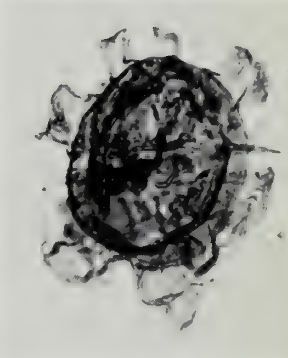

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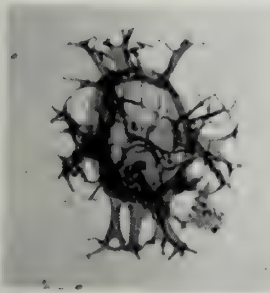

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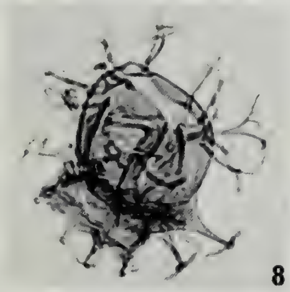

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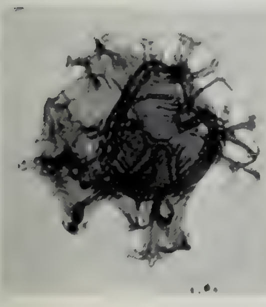

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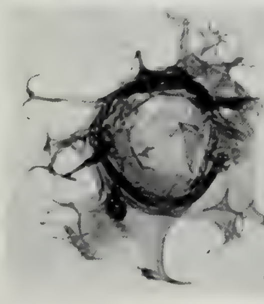

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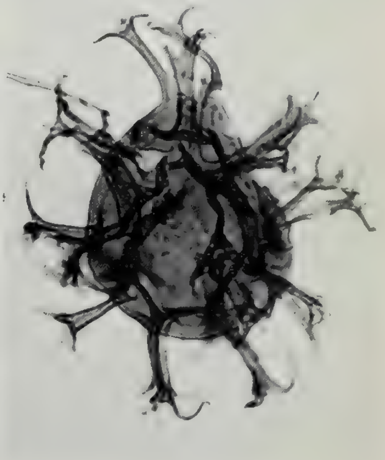

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PLATE 2

Adnatosphaeridium vittatum Williams & Downie 1966c (p. 238)

FIG. 1. Specimen V.57743 (1) ; W26A. × 500.

Adnatosphaeridium multispinosum Williams & Downie 1966c (p. 239)

FIG. 2. Specimen V.57780 (3) ; AB11. × 500.

Adnatosphaeridium robustum (Morgenroth 1966a) n. comb. (p. 239)

FIG. 3. Specimen V.57722 ; W5. × 500.

Cannosphaeropsis reticulensis Pastiels 1948 (p. 250)

FIG. 4. Specimen showing precingular archaeopyle. V.57780 (1) ; AB11. × 500.

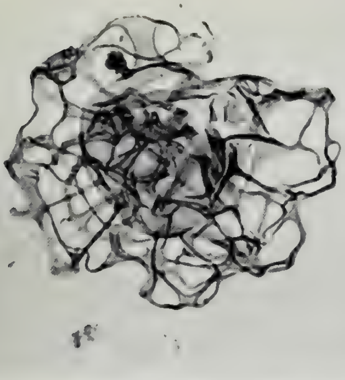
Araneosphaera araneosa gen. et sp. nov. (p. 240)

FIG. 5. Upper (dorsal) surface of specimen showing precingular archaeopyle. V.57797 (1) ; AB40. × 500.

FIG. 6. Holotype V.57765 (2) ; W56. × 500.

FIG. 7. Specimen showing cingular zone devoid of processes. V.57793 (1) ; AB40. × 500.

FIG. 8. Specimen V.57796 ; AB40. × 500.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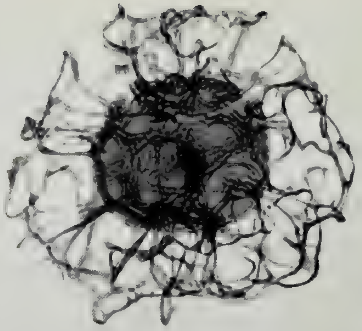
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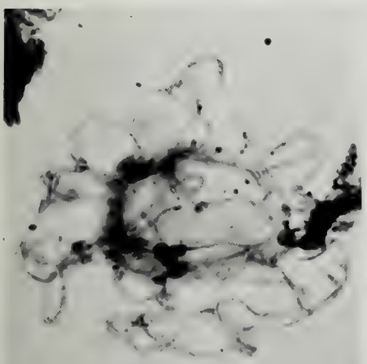
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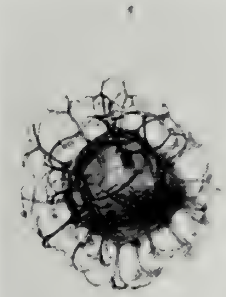
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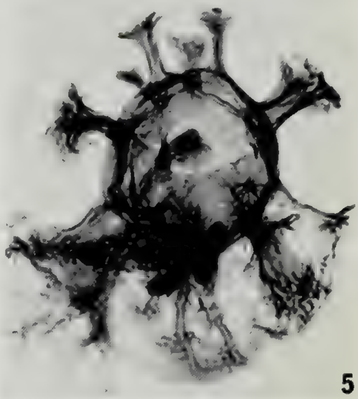
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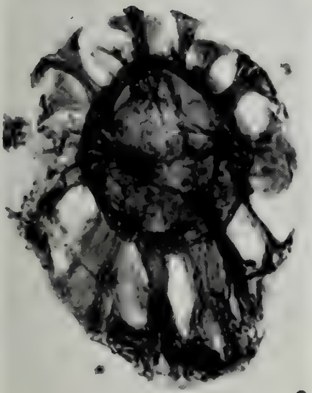
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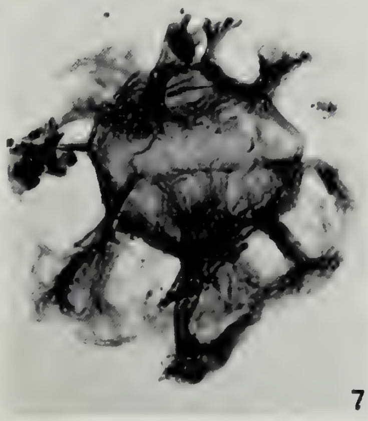
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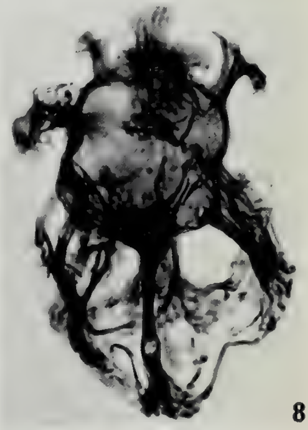
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PLATE 3

Areoligera senonensis Lejeune-Carpentier 1938 (p. 244)

Fig. 1. Specimen V.57728 (1); W13. × 500.

Areoligera coronata (O. Wetzel) Lejeune-Carpentier 1938 (p. 245)

Fig. 2. Upper (dorsal) surface of specimen showing process complexes. V.57729 (4); W13. × 500.

Areoligera medusettiformis (O. Wetzel) Lejeune-Carpentier 1938 (p. 245)

Fig. 3. Specimen V.57720 (2); W4. × 500.

Areoligera cf. **senonensis** Lejeune-Carpentier 1938 (p. 244)

Fig. 4. Lower (ventral) surface of specimen showing process complexes. V.57730 (5); W13. × 500.

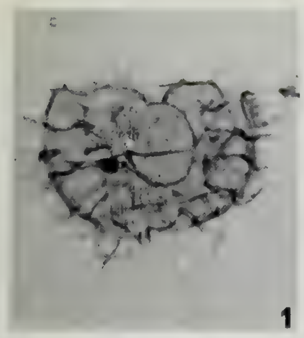
Fig. 5. Upper (dorsal) surface of same specimen. × 500.

Areoligera cf. **coronata** (O. Wetzel) Lejeune-Carpentier 1938 (p. 245)

Fig. 6. Specimen V.57729 (5); W13. × 500.

Areoligera cf. **medusettiformis** (O. Wetzel) Lejeune-Carpentier 1938 (p. 246)

Fig. 7. Specimen V.57729 (6); W13. × 500.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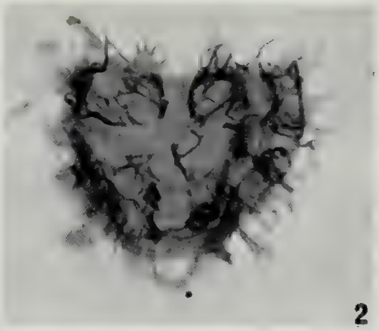
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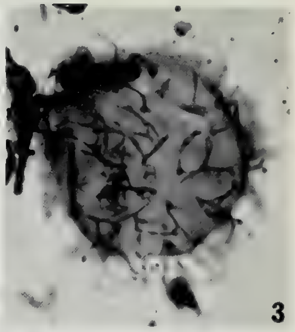
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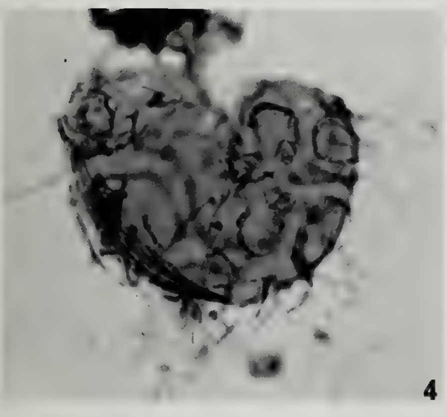
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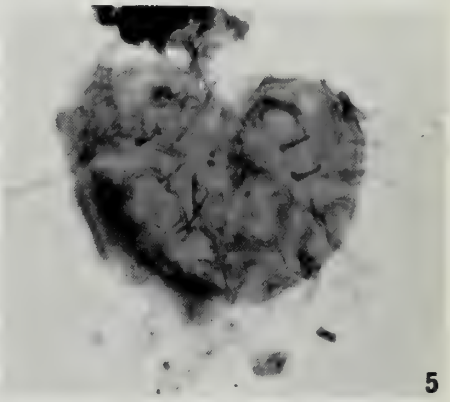
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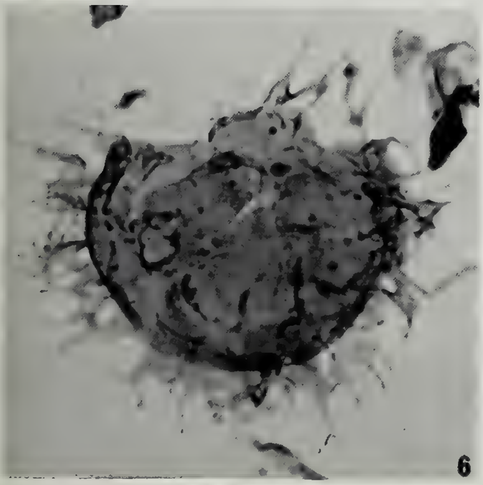
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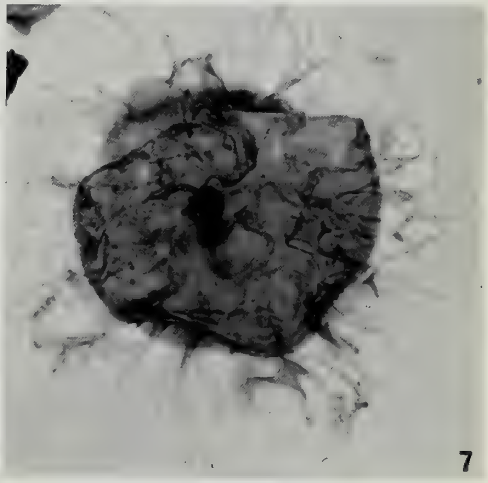
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PLATE 4

Areoligera sentosa n. sp. (p. 246 ; see also Pl. 5, figs 1, 3)

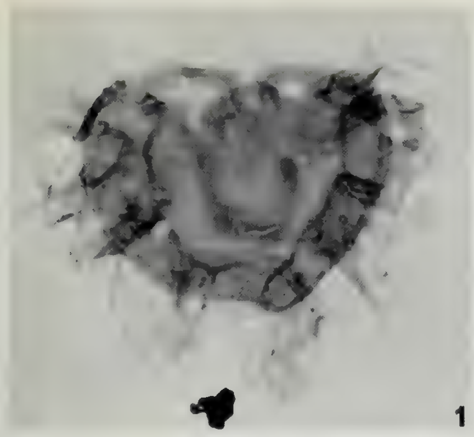
Fig. 1. Upper (ventral) surface of holotype. V.57794 (5) ; AB40. × 500.
Fig. 2. Lower (dorsal) surface of same specimen. × 500.

Areoligera tauloma n. sp. (p. 247 ; see also Pl. 5, figs 5, 6)

Fig. 3. Upper (ventral) surface of holotype. V.57768 (3) ; W57. × 500.
Fig. 5. Lower (dorsal) surface of same specimen. × 500.

Areoligera undulata n. sp. (p. 248 ; see also Pl. 5, figs 2, 4)

Fig. 4. Upper (ventral) surface of holotype. V.57802 (3) ; AB44. × 500.
Fig. 6. Lower (dorsal) surface of same specimen. × 500.



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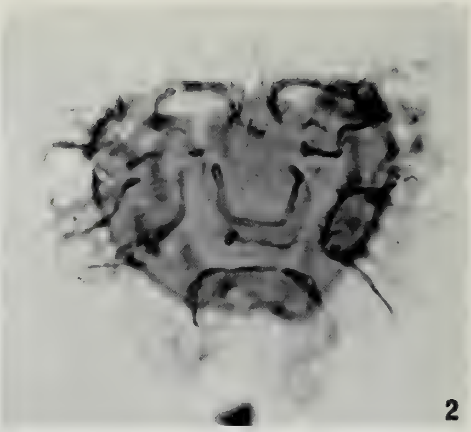

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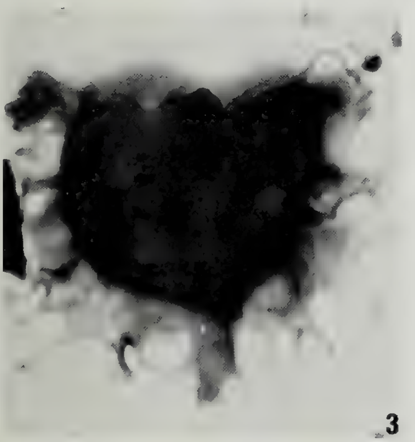

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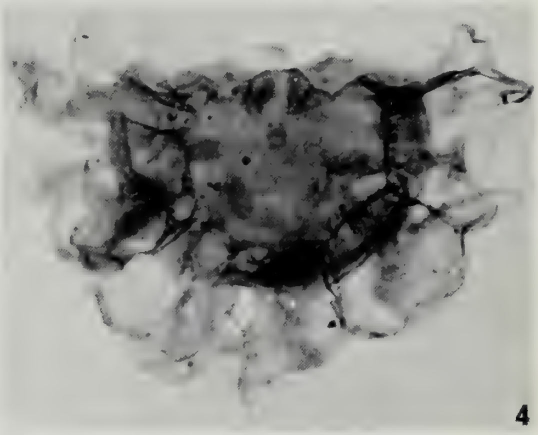

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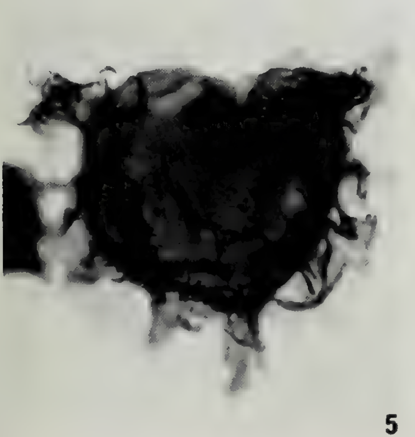

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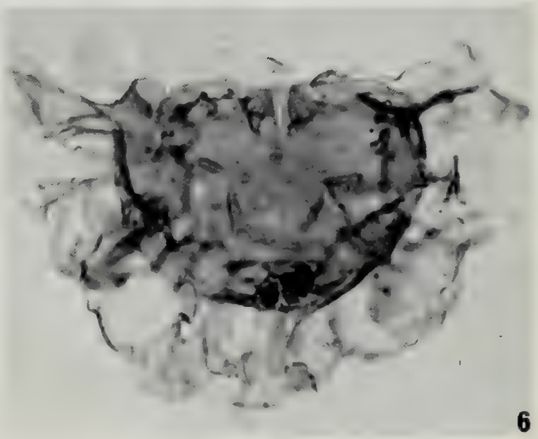

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PLATE 5

Areoligera sentosa n. sp. (p. 246 ; see also Pl. 4, figs 1, 2)

FIG. 1. Complete specimen. V.57767 (3) ; W56. × 500.

FIG. 3. Lower (dorsal) surface of specimen. V.57790 (3) ; AB40. × 500.

Areoligera undulata n. sp. (p. 248 ; see also Pl. 4, figs 4, 6)

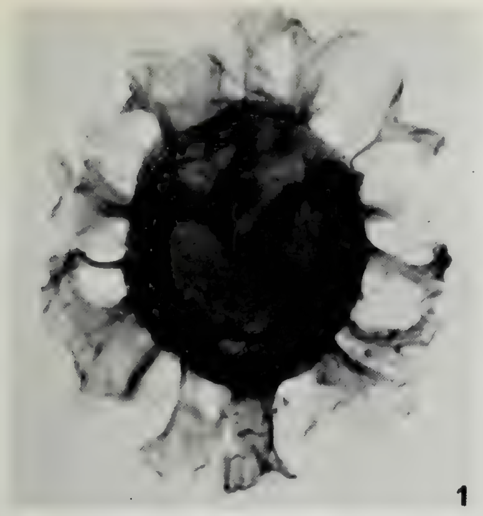
FIG. 2. Specimen V.57800 (2) ; AB44. × 500.

FIG. 4. Complete specimen. V.57795 (6) ; AB40. × 500.

Areoligera tauloma n. sp. (p. 247 ; see also Pl. 4, figs 3, 5)

FIG. 5. Upper (ventral) surface of specimen. V.57764 (4) ; W56. × 500.

FIG. 6. Lower (dorsal) surface of same specimen. × 500.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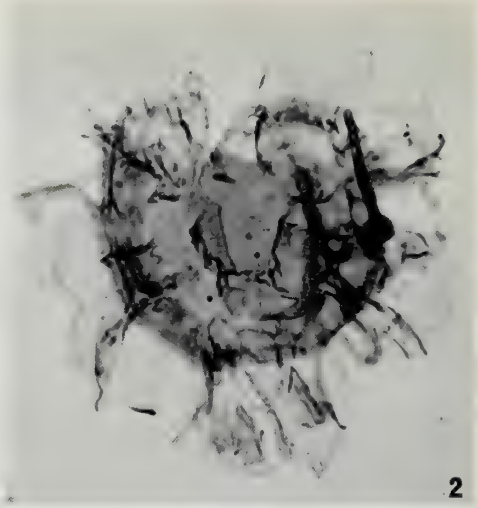
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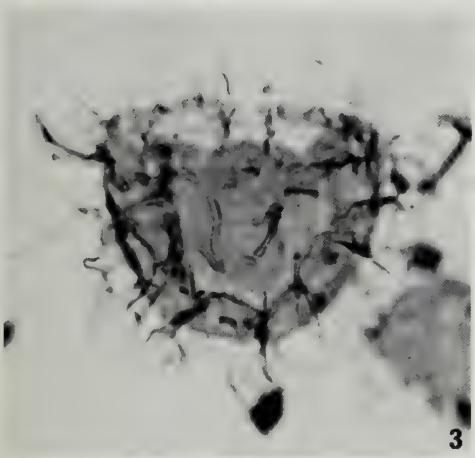
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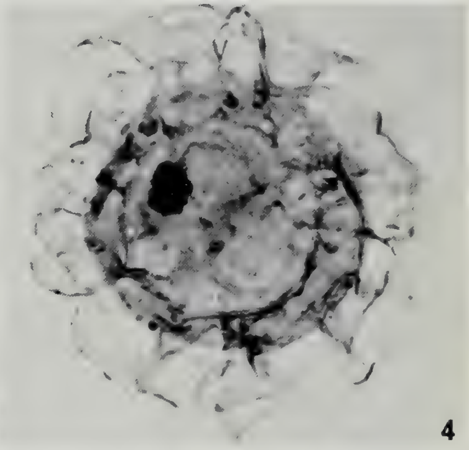
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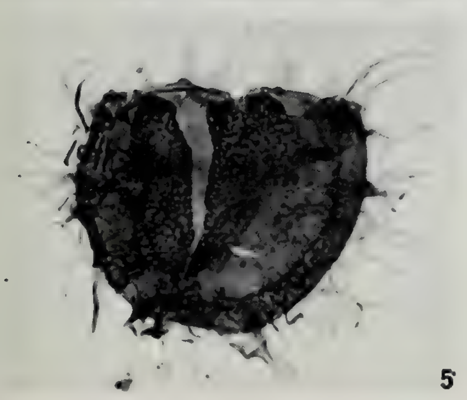
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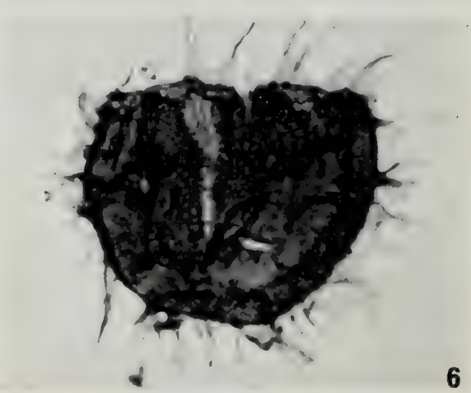
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PLATE 6

Areosphaeridium arcuatum Eaton 1971a (p. 250)

FIG. 1. Specimen V.57760 (1); W51. ×500.

Areosphaeridium diktyoplokus (Klumpp) Eaton 1971a (p. 249)

FIG. 2. Polar view showing apical archaeopyle. V.57759 (19); W51. ×500.

Areosphaeridium multicornutum Eaton 1971a (p. 250)

FIG. 3. Specimen V.57772 (8); W58. ×500.

Cordosphaeridium multispinosum Davey & Williams 1966b (p. 254)

FIG. 4. Specimen showing precingular archaeopyle. V.57783 (5); AB11. ×500.

Cordosphaeridium inodes (Klumpp) Eisenack 1963b emend. Morgenroth 1968 (p. 252)

FIG. 5. Specimen V.57801; AB44. ×500.

Cordosphaeridium fibrospinosum Davey & Williams 1966b (p. 253)

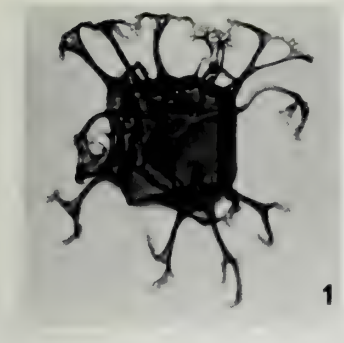
FIG. 6. Specimen V.57783 (1); AB11. ×500.

Cordosphaeridium gracilis (Eisenack) Davey & Williams 1966b (p. 253)

FIG. 7. Specimen with characteristic Y-shaped process. V.57737 (3); W18. ×500.

Cordosphaeridium exilimurum Davey & Williams 1966b (p. 253)

FIG. 8. Specimen V.57781 (4); AB11. ×500.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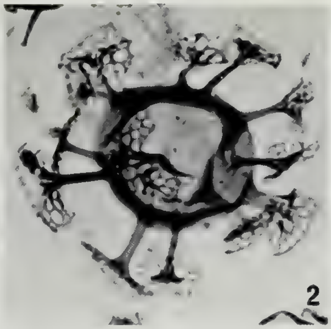
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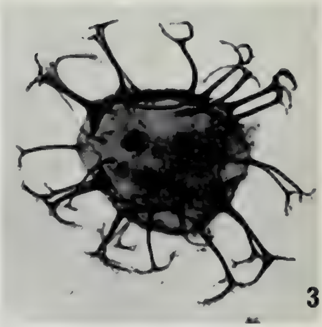
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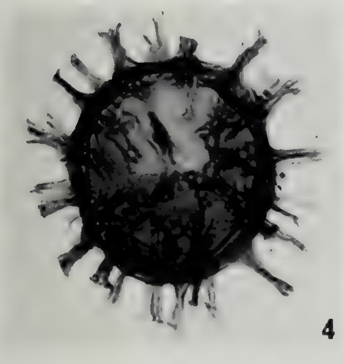
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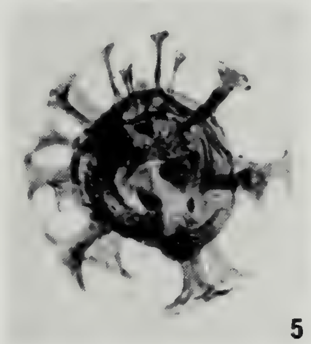
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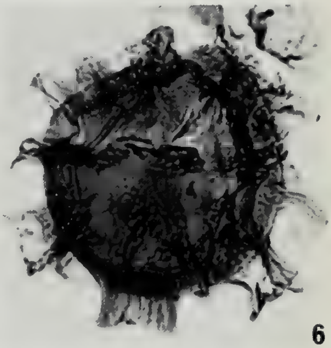
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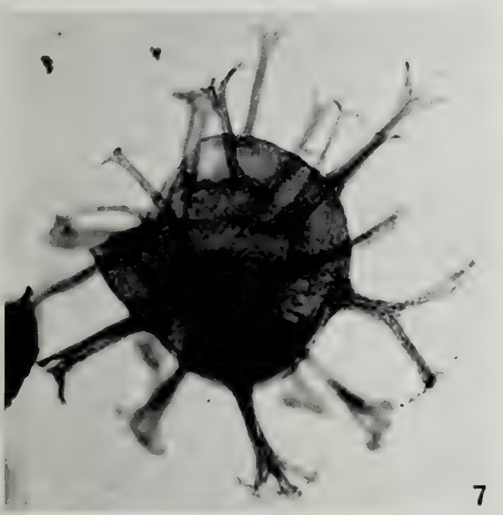
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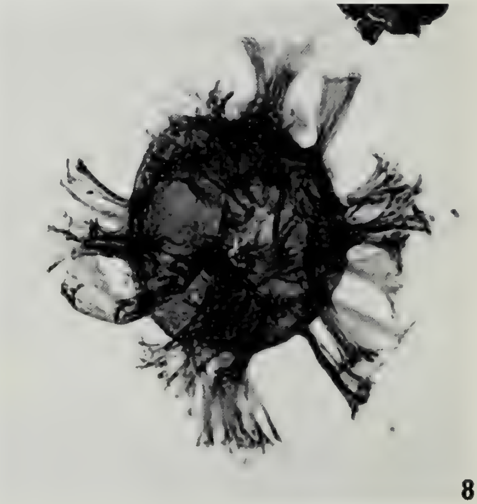
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PLATE 7

Cordosphaeridium ? minimum (Morgenroth) Benedek 1972 (p. 254)

FIG. 1. Specimen V.57763 (4) ; W56. × 1000.

FIG. 2. Same specimen showing process ribs extending to the distal margin of the processes. × 1000.

FIG. 3. Specimen showing process ribs. V.57747 (1) ; W30. × 1000.

Chiropteridium* cf. *dispersum Gocht 1960 (p. 251)

FIG. 4. Specimen V.57753 (2) ; W38. × 500.

Cyclonephelium divaricatum Williams & Downie 1966c (p. 255)

FIG. 5. Specimen V.57747 (2) ; W30. × 500.

Cyclonephelium laciniiforme Gerlach 1961 (p. 257)

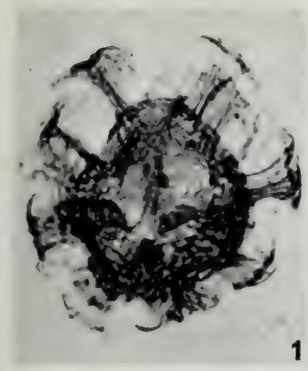
FIG. 6. Specimen V.57799 (3) ; AB42. × 500.

Cyclonephelium* aff. *exuberans Deflandre & Cookson 1955 *ex* Eaton 1976 (p. 256)

FIG. 7. Complete specimen V.57727 (4) ; W13. × 500.

Cyclonephelium ordinatum Williams & Downie 1966c (p. 258)

FIG. 8. Complete specimen. V.57738 (1) ; W20. × 500.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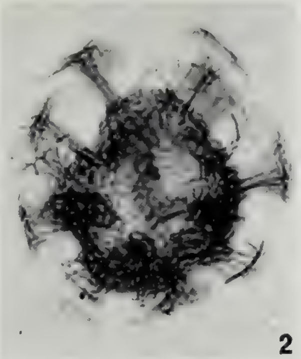
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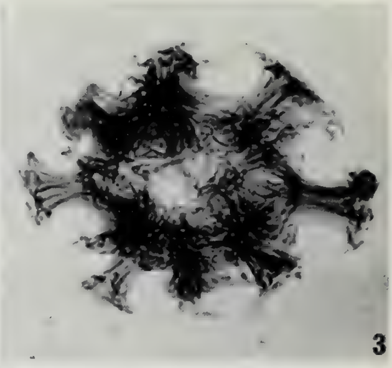
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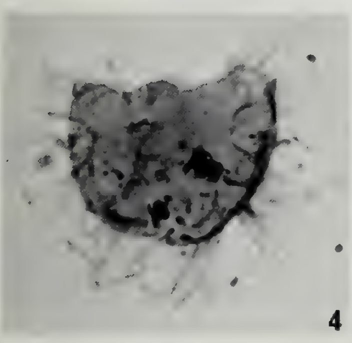
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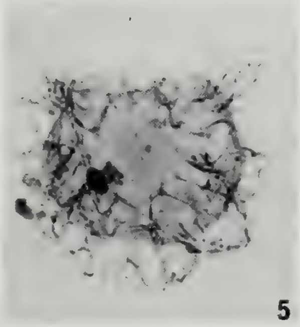
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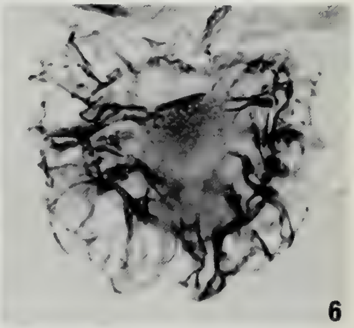
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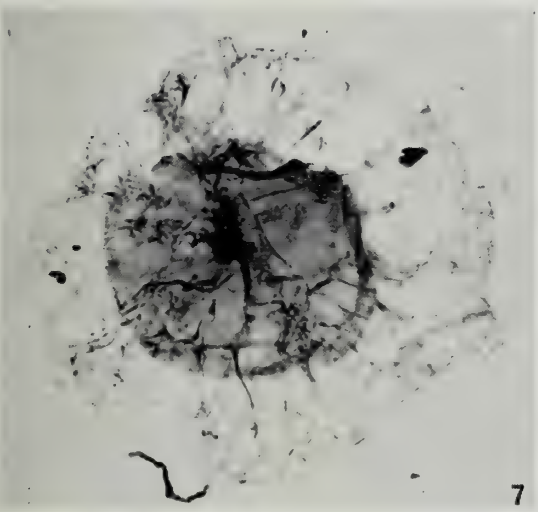
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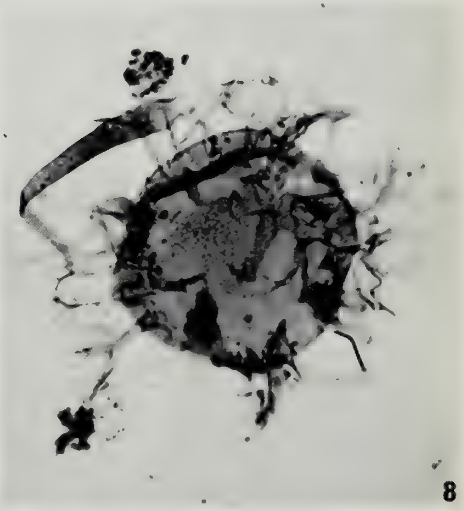
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PLATE 8

Cyclonephelium exuberans Deflandre & Cookson 1955 (p. 255)

FIG. 1. Complete specimen. V.57758 (5) ; W40. × 500.

FIG. 2. Specimen showing the absence of processes on reflected plates 3″ and 6″. V.57757 (10) ; W40. × 500.

Cyclonephelium spinetum n. sp. (p. 259)

FIG. 3. Holotype V.57742 ; W26A. × 500.

Cyclonephelium vicinum n. sp. (p. 260)

FIG. 4. Holotype V.57744 ; W26A. × 500.

FIG. 5. Complete specimen V.57789 (2) ; AB28. × 500.

Cyclonephelium intricatum Eaton 1971a (p. 257)

FIG. 6. Specimen V.57798 (3) ; AB42. × 500.

Diphyes colligerum (Deflandre & Cookson) Cookson 1965
emend. Davey & Williams 1966b (p. 262)

FIG. 7. Specimen V.57724 (1) ; W6. × 500.

Eocladopyxis peniculatum Morgenroth 1966a (p. 266)

FIG. 8. Specimen showing apical archaeopyle and separation of the precingular and cingular plates. V.57739 (2) ; W22. × 500.

Gonyaulacysta tenuitabulata (Gerlach) De Coninck 1968 (p. 266)

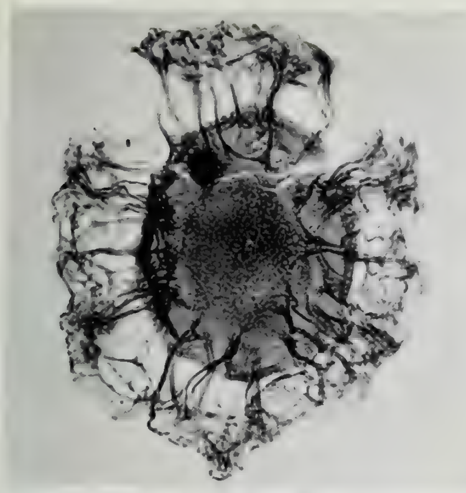
FIG. 9. Specimen showing precingular archaeopyle. V.57770 (2) ; W58. × 500.

Lingulodinium machaerophorum (Deflandre & Cookson) Wall 1967 (p. 276)

FIG. 10. Specimen V.57794 (6) ; AB40. × 500.

Leptodinium membranigerum Gerlach 1961 (p. 276)

FIG. 11. Specimen V.57791 (7) ; AB40. × 500.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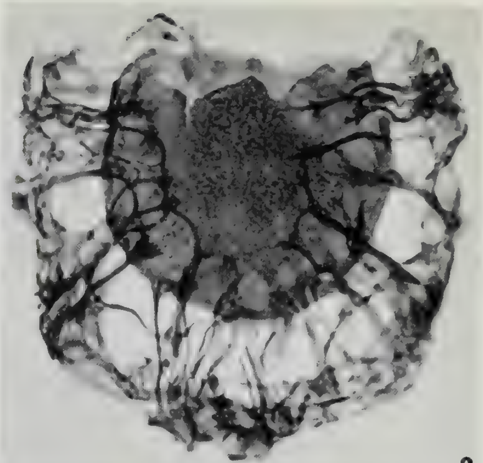
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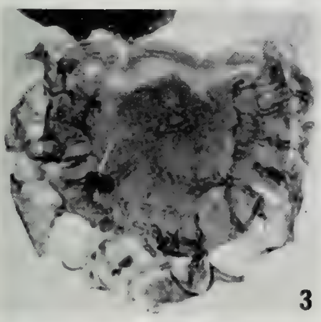
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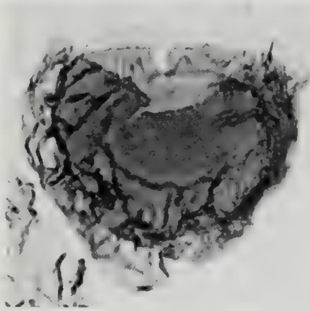
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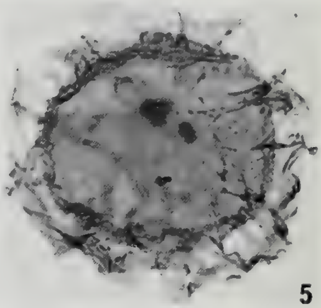
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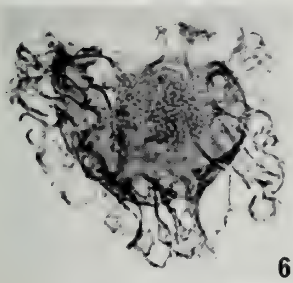
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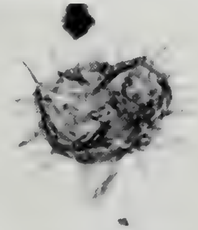
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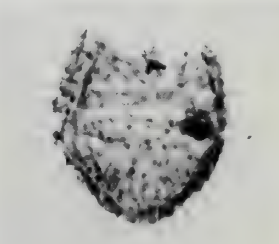
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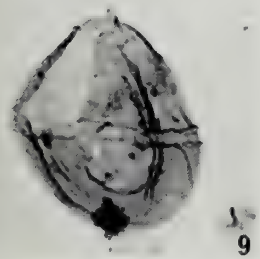
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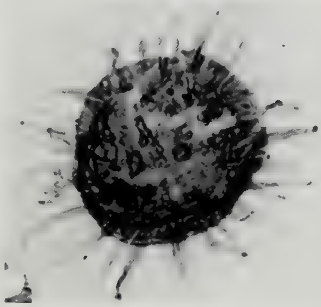
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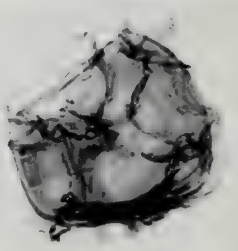
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PLATE 9

Distatodinium craterum gen. et sp. nov. (p. 263)

Fig. 1. Holotype V.57792 ; AB40. × 500.

Fig. 2. Specimen V.57793 (2) ; AB40. × 500.

Fig. 3. Specimen V.57762 (2) ; W55. × 500.

Fig. 4. Specimen with three longitudinally aligned processes proximally united by membrane. V.57793 (3) ; AB40. × 500.

Fig. 5. Specimen V.57791 (15) ; AB40. × 500.

Distatodinium paradoxum (Brosius 1963) n. comb. (p. 265)

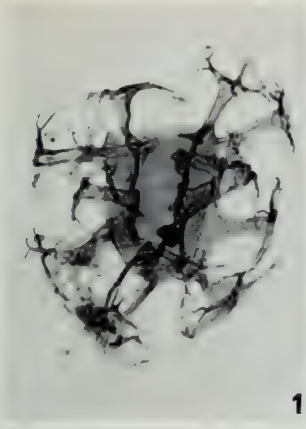
Fig. 6. Specimen showing partial detachment of the polar zone. V.57771 (3) ; W58. × 500.

Distatodinium ellipticum (Cookson 1965) n. comb. (p. 264)

Fig. 7. Specimen showing considerable development of membrane proximally uniting processes in the antapical zone. V.57802 (4) ; AB44. × 500.

Fig. 8. Specimen V.57766 (16) ; W56. × 500.

Fig. 9. Specimen V.57769 ; W57. × 500.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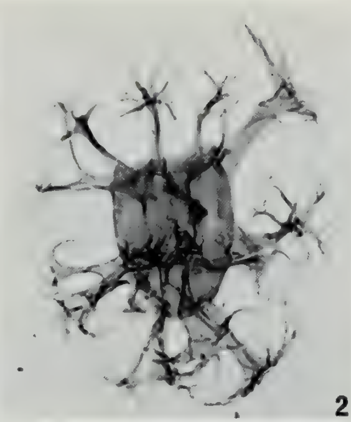
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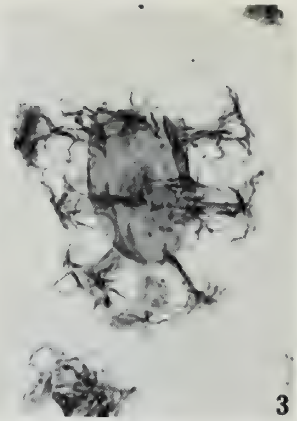
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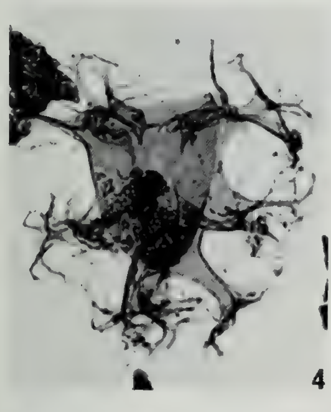
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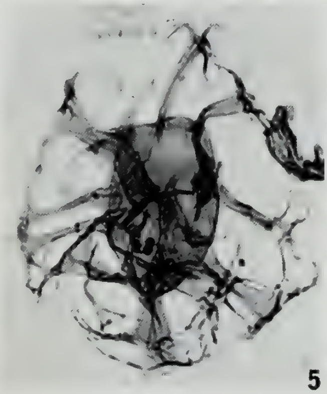
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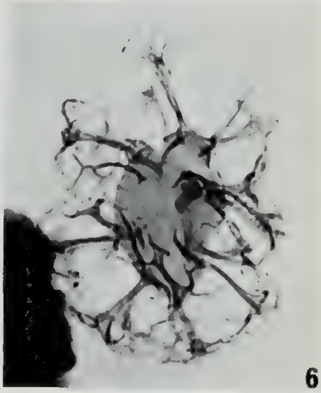
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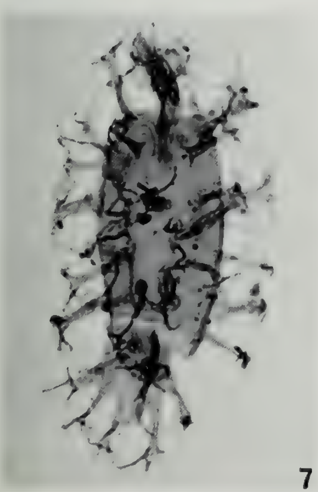
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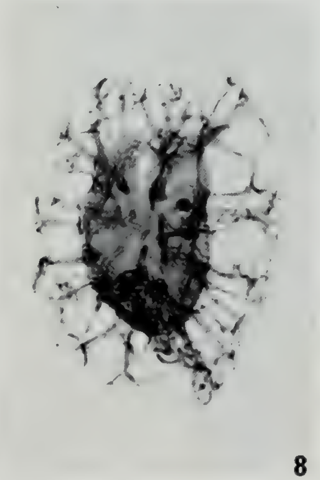
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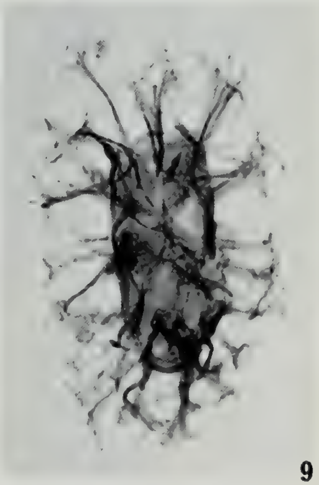
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PLATE 10

Homotryblium tenuispinosum Davey & Williams 1966b (p. 266)

Fig. 1. Specimen showing epitractal archaeopyle. V.57763 (12) ; W56. × 500.

Homotryblium abbreviatum n. sp. (p. 267)

Fig 2. Complete specimen V.57782 (3) ; AB11. × 500.

Fig. 3. Holotype V.57782 (1) ; AB11. × 500.

Fig. 4. Complete specimen showing separation of epitract and hypotract in archaeopyle formation. V.57781 (2) ; AB11. × 500.

Homotryblium oceanicum n. sp. (p. 268)

Fig. 5. Holotype V.57794 (1) ; AB40. × 500.

Fig. 6. Detached operculum with one particularly broad precingular process. V.57772(2) ; W58. × 500.

Fig. 7. Detached operculum. V.57772 (4) ; W58. × 500.

Fig. 8. Specimen V.57772 (5) ; W58. × 500.

Hystrichokolpoma eisenacki Williams & Downie 1966a (p. 268)

Fig. 9. Specimen V.57746 (3) ; W27. × 500.

Hystrichokolpoma rigaudae Deflandre & Cookson 1955 (p. 270)

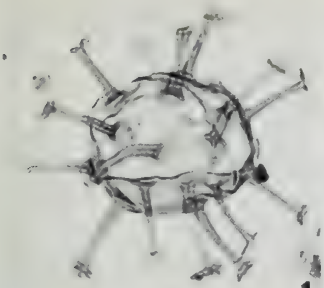
Fig. 10. Specimen showing characteristic distally expanded large processes. V.57803 (3) ; AB44. × 500.

Hystrichokolpoma granulata n. sp. (p. 269)

Fig. 11. Holotype V.57781 (6) ; AB11. × 500.

Fig. 12. Specimen V.57746 (4) ; W27. × 500.

Fig. 13. Polar view showing apical archaeopyle. V.57741 (1) ; W23. × 500.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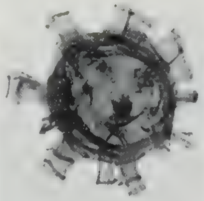
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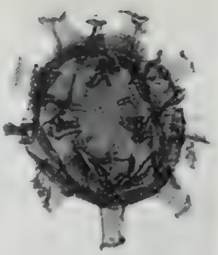
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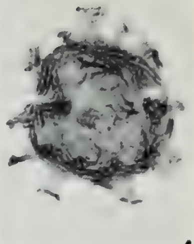
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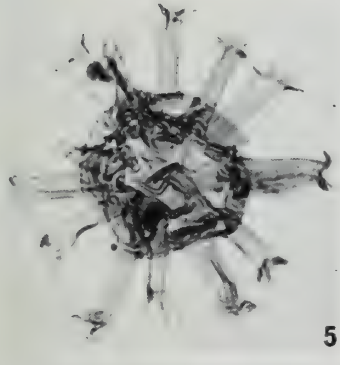
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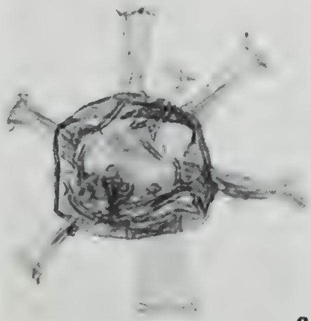
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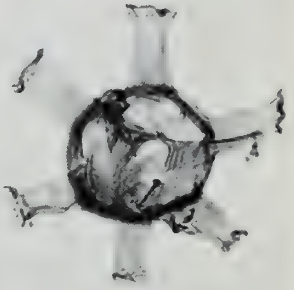
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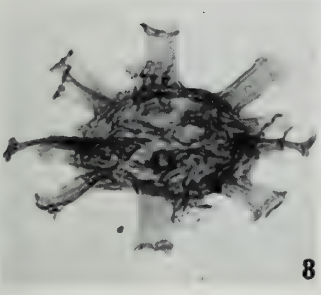
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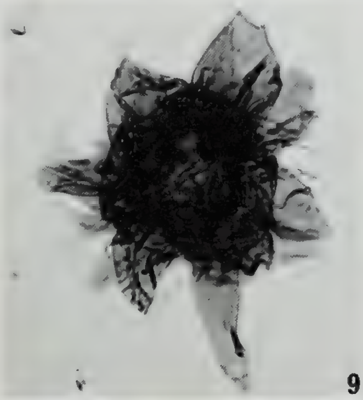
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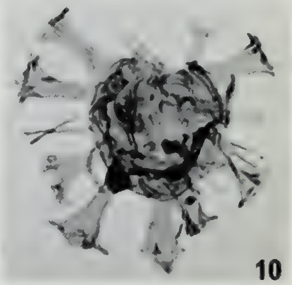
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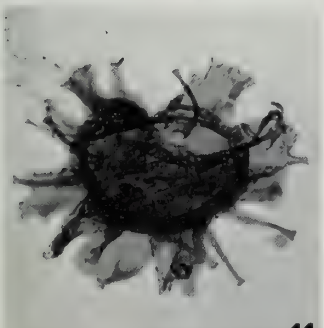
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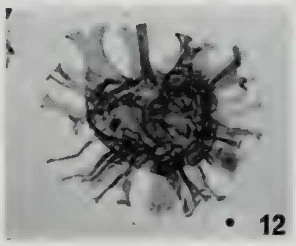
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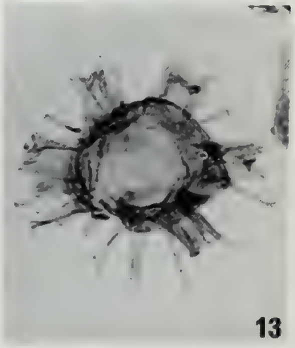
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PLATE 11

Hystrichokolpoma salacia n. sp. (p. 271)

Fig. 1. Holotype V.57757 (6) ; W40. × 500.
Fig. 2. Specimen V.57759 (10) ; W51. × 500.
Fig. 3. Specimen V.57756 (10) ; W40. × 500.

Hystrichosphaeridium tubiferum (Ehrenberg) Deflandre 1937 emend. Davey & Williams 1966b (p. 272)

Fig. 4. Specimen V.57778 (1) ; AB5. × 500.

Hystrichosphaeridium patulum Davey & Williams 1966b (p. 274)

Fig. 5. Specimen V.57791 (4) ; AB40. × 1000.

Hystrichosphaeridium pseudorecurvatum Morgenroth 1966a (p. 274)

Fig. 6. Specimen with more than one process per plate. V.57772 (1) ; W58. × 500.

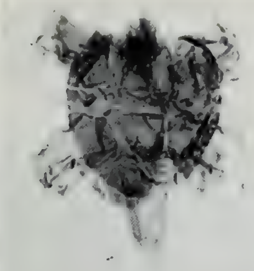
Hystrichosphaeridium asterium n. sp. (p. 273)

Fig. 7. Holotype V.57772 (3) ; W58. × 1000.

Fig. 8. Same specimen ; note the distinctive appearance of the distal part of the processes. × 1000.

Fig. 9. Specimen with one process showing considerable proximal expansion. V.57770 (1) ; W58. × 1000.

Fig. 10. Same specimen showing the characteristic form of the distal part of the processes. × 1000.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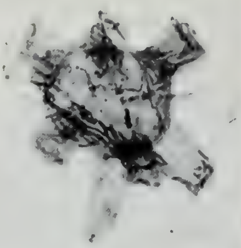
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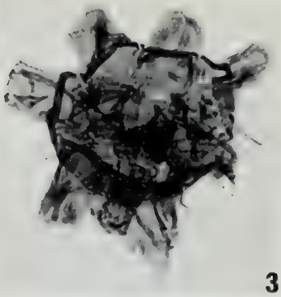
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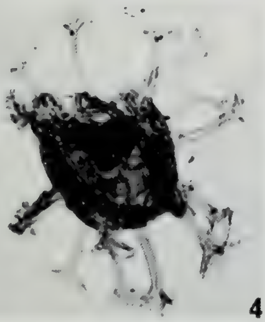
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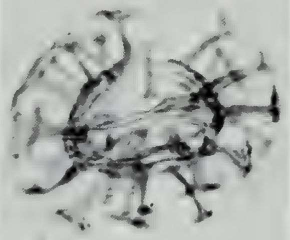
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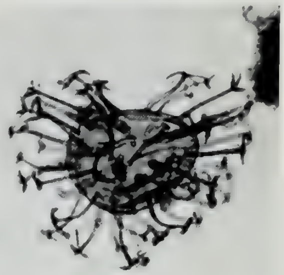
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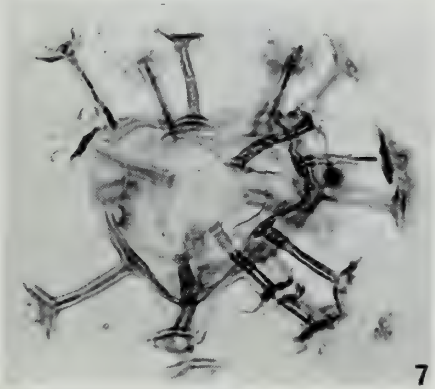
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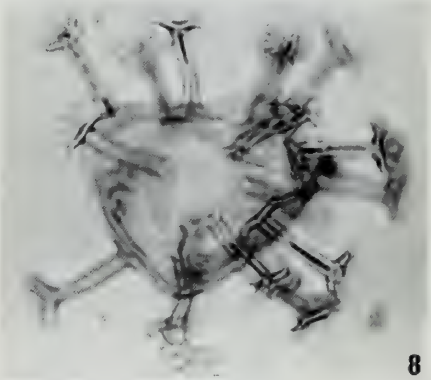
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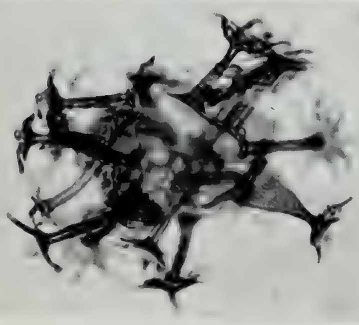
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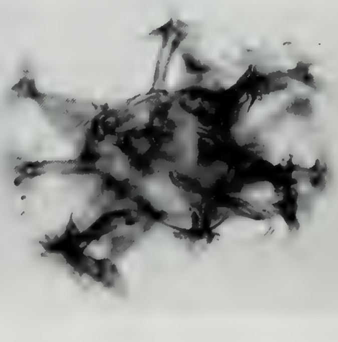
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PLATE 12

Lanternosphaeridium lanosum Morgenroth 1966a (p. 274)

Fig. 1. Specimen with distinct apical horn. V.57777 ; AB5. × 500.

Lanternosphaeridium axiale (Eisenack) Morgenroth 1966a (p. 275)

Fig. 2. Specimen showing precingular archaeopyle. V.57761 (3) ; W54. × 500.

Lanternosphaeridium radiatum Morgenroth 1966a (p. 275)

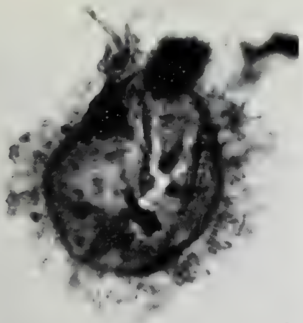
Fig. 3. Specimen showing precingular archaeopyle. V.57729 (2) ; W13. × 500.

Lanternosphaeridium vectense n. sp. (p. 275)

Fig. 4. Holotype, lateral view. V.57797 (2) ; AB40. × 500.
Fig. 5. Specimen V.57795 (4) ; AB40. × 500.
Fig. 6. Specimen showing precingular archaeopyle. V.57799 (2) ; AB42. × 500.

Membranilarnacia ursulae (Morgenroth) De Coninck 1968 (p. 277)

Fig. 7. Specimen V.57778 (2) ; AB5. × 500.



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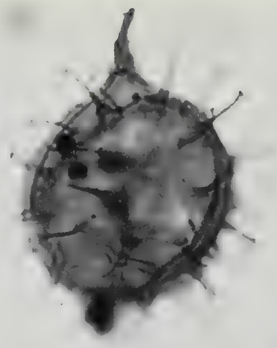

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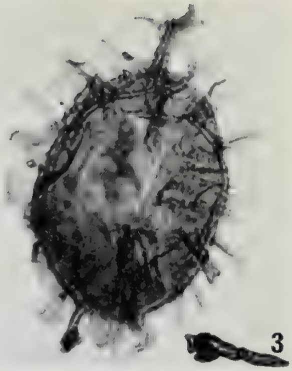

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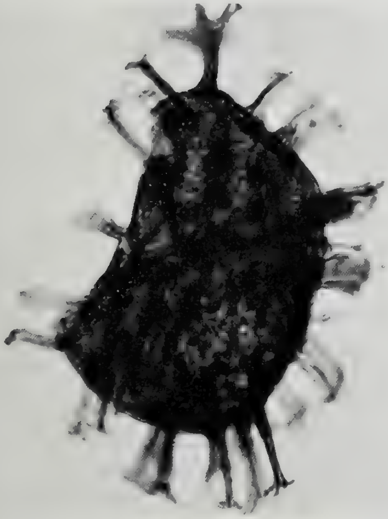

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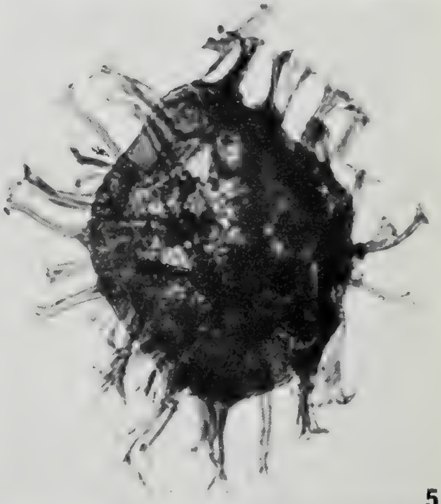

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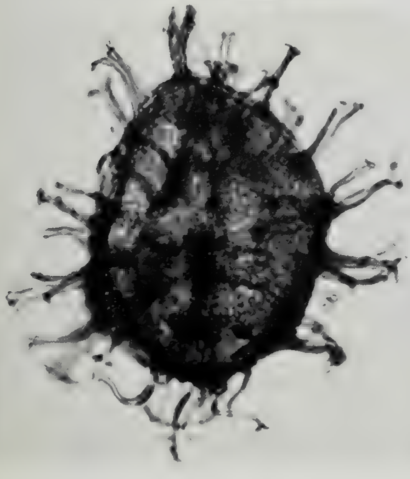

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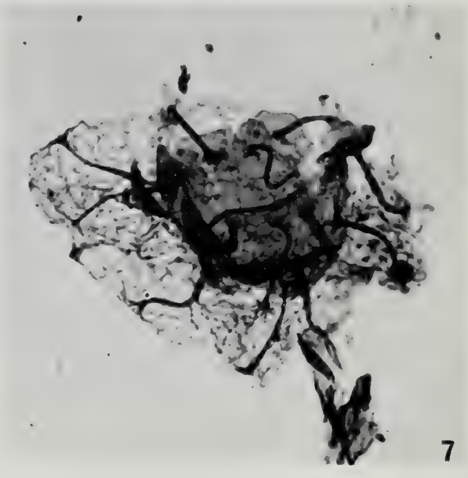

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PLATE 13

Litosphaeridium ? inversibuccinum Davey & Williams 1966b (p. 278)

FIG. 1. Specimen V.57763 (6) ; W56. × 1000.

FIG. 2. Same specimen showing apical archaeopyle. × 1000.

FIG. 3. Upper surface of specimen showing apical archaeopyle. V.57735 (4) ; W18. × 1000.

FIG. 4. Same specimen ; mid-focus showing precingular processes. × 1000.

FIG. 5. Lower surface of same specimen showing postcingular processes. × 1000.

Pentadinium laticinctum Gerlach 1961 (p. 279)

FIG. 6. Lower surface of specimen showing apical plates. V.57752 ; W37. × 500.

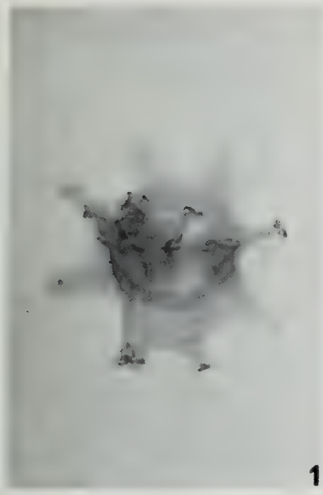
FIG. 7. Same specimen, mid-focus. × 500.

FIG. 8. Upper surface of same specimen showing antapical plate. × 500.

FIG. 9. Upper (ventral) surface of specimen. V.57750 (4) ; W32. × 500.

FIG. 10. Same specimen, mid-focus. × 500.

FIG. 11. Lower (dorsal) surface of same specimen showing precingular archaeopyle. × 500.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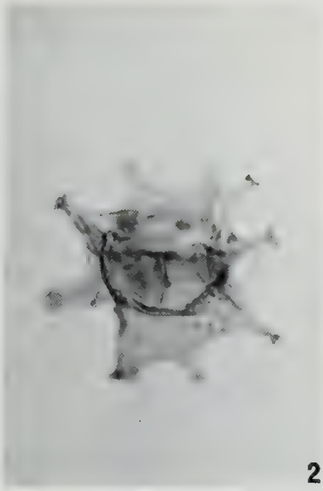
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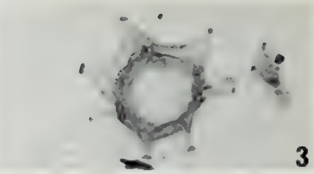
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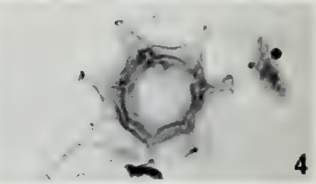
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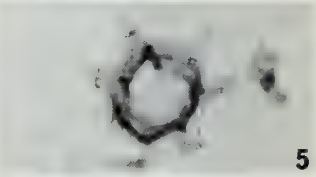
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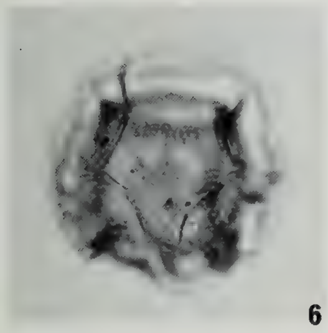
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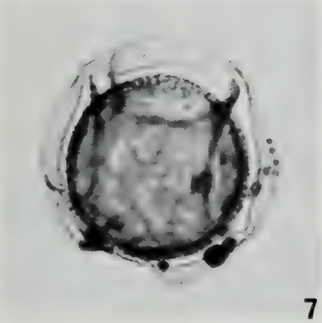
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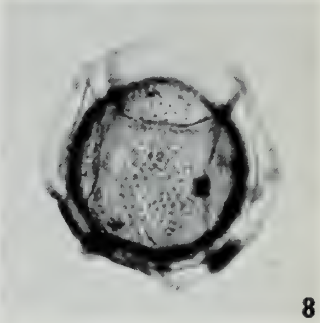
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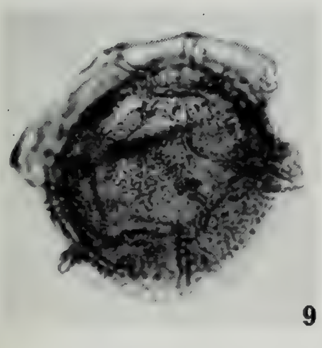
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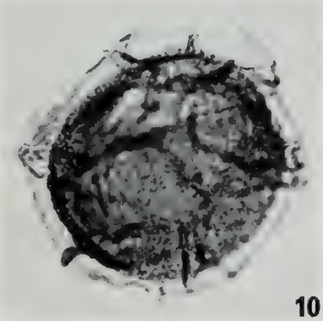
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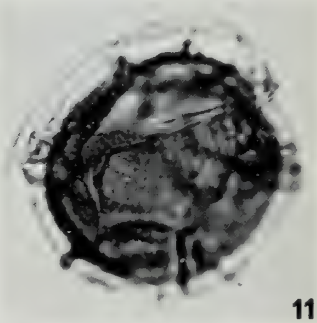
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PLATE 14

Polysphaeridium subtile Davey & Williams 1966b (p. 280)

Fig. 1. Specimen V.57732 (2) ; W17. × 500.

Fig. 2. Specimen showing epitractal archaeopyle. V.57735 (3) ; W18. × 500.

Spiniferites ramosus var. **ramosus** Davey & Williams 1966a (p. 281)

Fig. 3. Specimen V.57759 (6) ; W51. × 500.

Spiniferites ramosus var. **granosus** Davey & Williams 1966a (p. 281)

Fig. 4. Specimen V.57773 (3) ; AB1. × 500.

Spiniferites ramosus var. **granomembranaceus** Davey & Williams 1966a (p. 281)

Fig. 5. Specimen V.57786 (2) ; AB18. × 500.

Spiniferites ramosus var. **multibrevis** Davey & Williams 1966a (p. 281)

Fig. 6. Specimen V.57734 (1) ; W17. × 500.

Spiniferites ramosus var. **membranaceus** (Rossignol) Davey & Williams 1966a (p. 281)

Fig. 7. Specimen V.57759 (7) ; W51. × 500.

Spiniferites monilis (Davey & Williams) Sarjeant 1970 emend. (p. 282)

Fig. 8. Specimen showing precingular archaeopyle. V.57787 ; AB18. × 500.

Fig. 9. Specimen V.57759 (9) ; W51. × 500.

Spiniferites cornutus (Gerlach) Sarjeant 1970 (p. 282)

Fig. 10. Specimen showing precingular archaeopyle. V.57766 (4) ; W56. × 500.

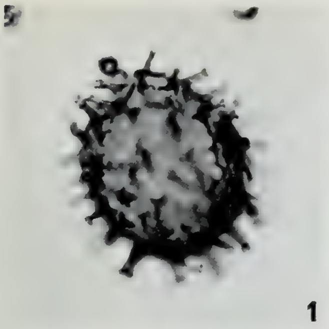
Spiniferites cingulatus (O. Wetzel) Sarjeant 1970 (p. 281)

Fig. 11. Specimen V.57776 (1) ; AB4A. × 500.

Spiniferites pseudofurcatus (Klumpp) Sarjeant 1970 (p. 283)

Fig. 12. Specimen V.57765 (3) ; W56. × 500.

Fig. 13. Specimen V.57760 (3) ; W51. × 500.



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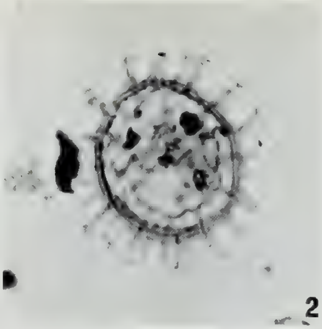

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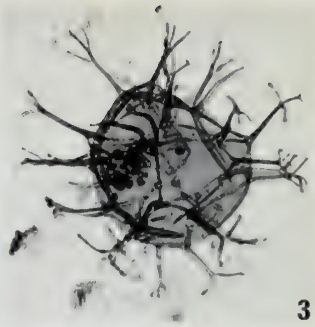

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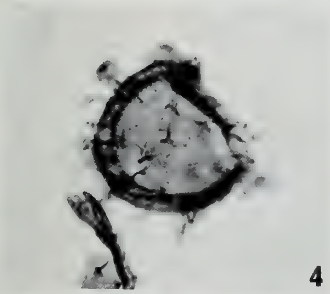

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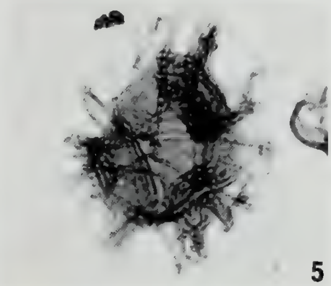

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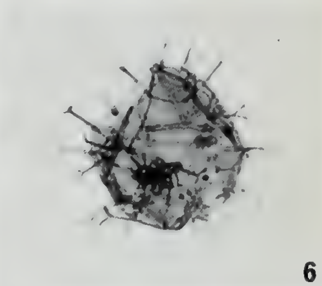

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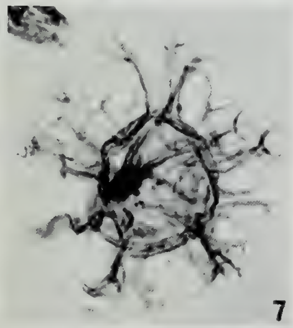

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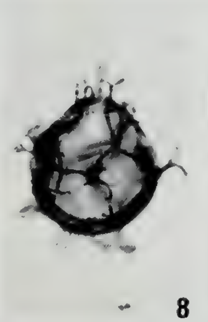

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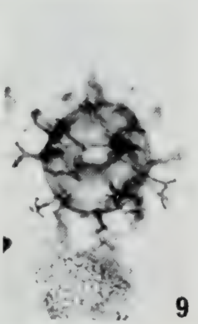

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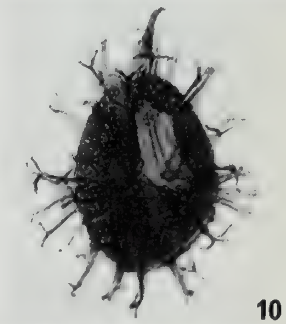

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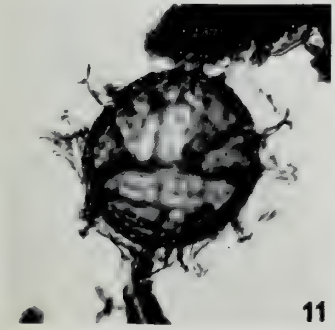

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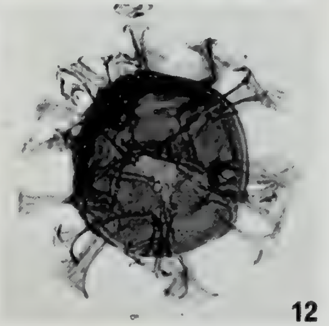

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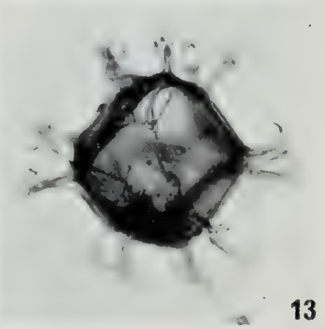

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PLATE 15

Operculodinium centrocarpum (Deflandre & Cookson) Wall 1967 (p. 278)

FIG. 1. Lower (dorsal) surface of specimen showing precingular archaeopyle. V.57748 (1); W31. × 1000.

FIG. 2. Upper (ventral) surface of same specimen. × 1000.

Samlandia chlamydophora Eisenack 1954 (p. 281)

FIG. 3. Lateral view of specimen. V.57766 (1); W56. × 500.

Turbiosphaera galatea n. sp. (p. 289)

FIG. 4. Holotype. V.57783 (4); AB11. × 500.

FIG. 5. Lateral view of specimen. V.57783 (3); AB11. × 500.

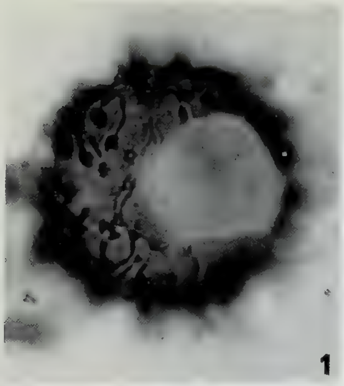
FIG. 6. Specimen V.57781 (3); AB11. × 500.

Turbiosphaera magnifica n. sp. (p. 290)

FIG. 7. Specimen V.57757 (4); W40. × 500.

FIG. 8. Holotype. V.57756 (7); W40. × 500.

FIG. 9. Specimen showing precingular archaeopyle. V.57757 (3); W40. × 500.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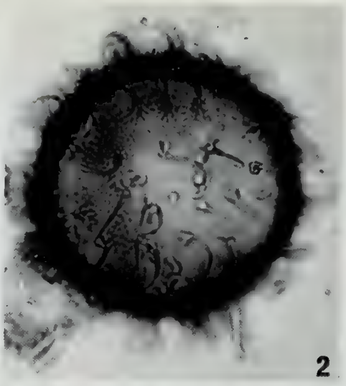
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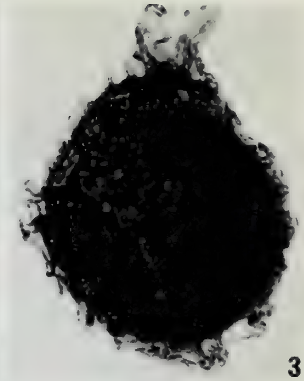
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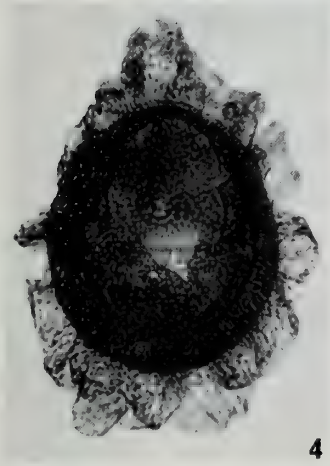
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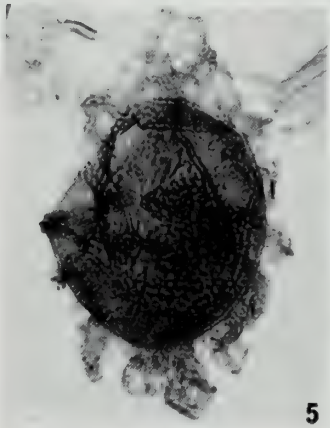
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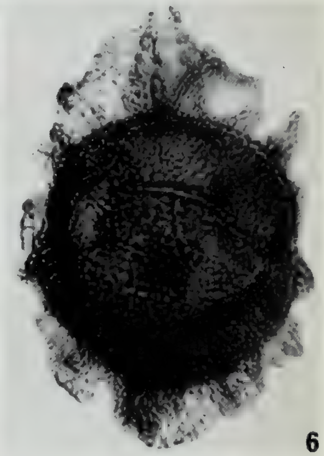
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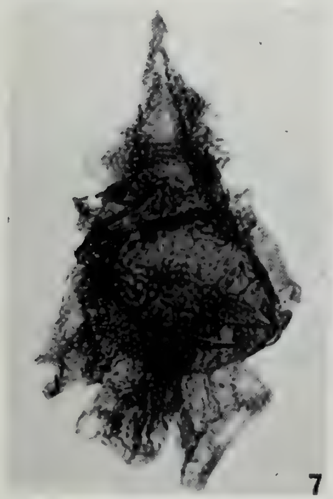
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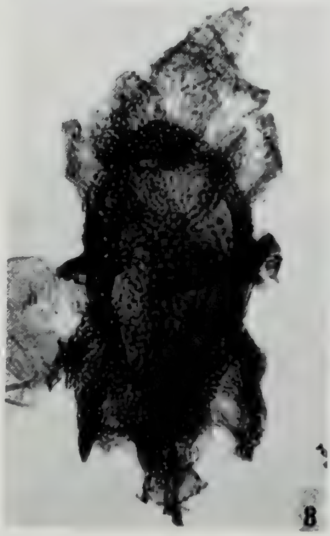
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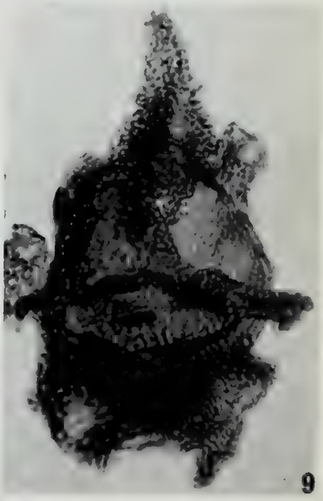
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PLATE 16

Thalassiphora delicata Williams & Downie 1966c emend. (p. 287)

Fig. 1. Specimen with ventral surface uppermost, showing large opening formed by the displacement of plate 1″, and precingular archaeopyle on the lower (dorsal) surface. V.57767 (1) ; W56. × 500.

Fig. 2. Specimen with dorsal surface uppermost. V.57790 (2) ; AB40. × 500.

Fig. 3. Specimen with dorsal surface uppermost. V.57766 (9) ; W56. × 500.

Thalassiphora pelagica (Eisenack) Eisenack & Gocht 1960 (p. 286)

Fig. 4. Specimen showing precingular archaeopyle and antapical keel. V.57783 (2) ; AB11. × 250.

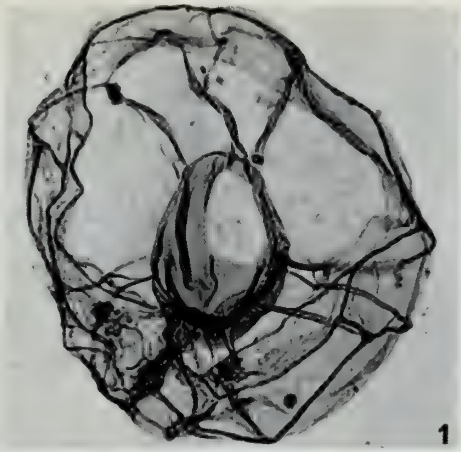
Fig. 5. Lateral view of complete specimen. V.57736 (3) ; W18. × 450.

Deflandrea depressa Morgenroth 1966a (p. 291)

Fig 6. Specimen V.57756 (8) ; W40. × 1000.

Palaeocystodinium golzowense Alberti 1961 (p. 294)

Fig. 7. Specimen showing intercalary archaeopyle. V.57733 (2) ; W17. × 500.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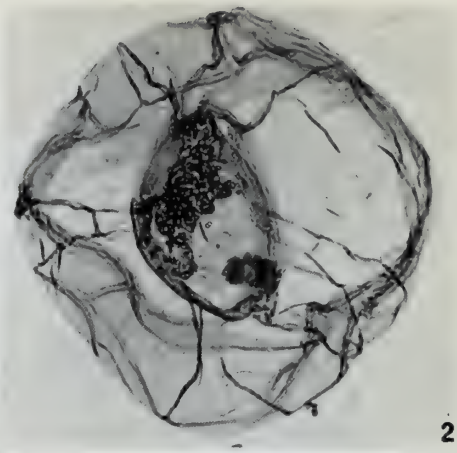
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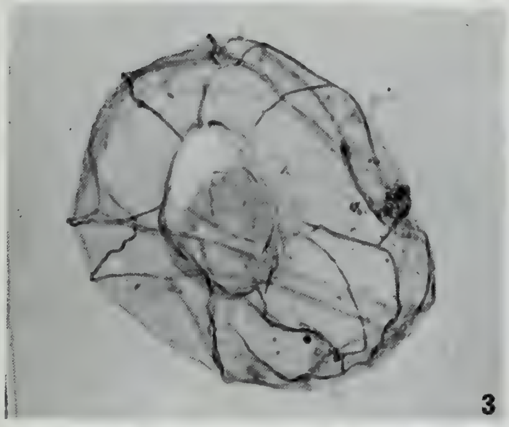
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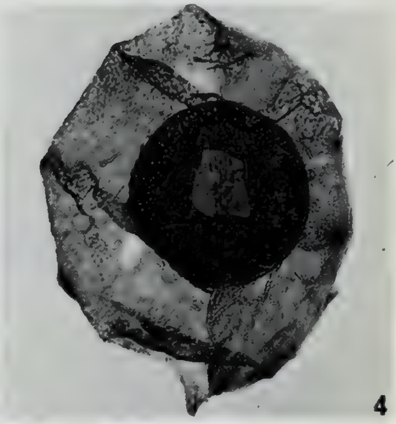
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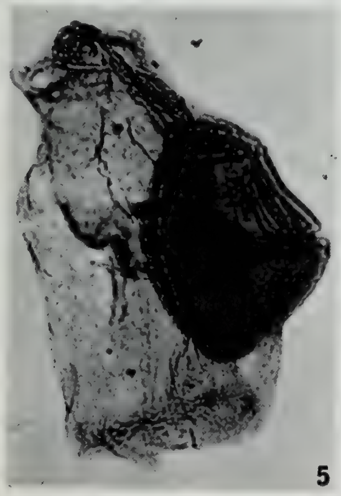
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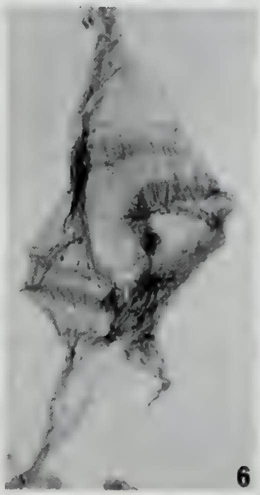
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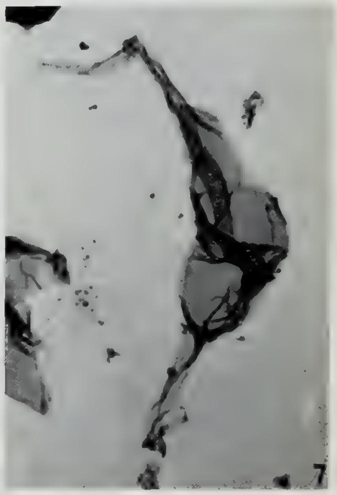
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PLATE 17

Deflandrea phosphoritica Eisenack 1938 (p. 290)

FIG. 1. Specimen V.57771 (2); W58. × 500.

Phthanoperidinium tritonium n. sp. (p. 299)

FIG. 2. Specimen showing intercalary archaeopyle. V.57790 (7); AB40. × 1000.

FIG. 3. Holotype. V.57756 (14); W40. × 1000.

FIG. 6. Specimen showing well-developed sutural crests. V.57749 (2); W32. × 1000.

FIG. 7. Specimen showing intercalary archaeopyle and additional displacement of plate 4″. V.57747 (6); W30. × 1000.

Deflandrea wetzeli Morgenroth 1966a (p. 292)

FIG. 4. Specimen showing large intercalary archaeopyle. V.57721 (1); W4. × 500.

Lejeunia hyalina Gerlach 1961 (p. 293)

FIG. 5. Specimen V.57735 (1); W18. × 500.

Phthanoperidinium echinatum n. sp. (p. 298)

FIG. 8. Upper (ventral) surface of holotype. V.57755 (4); W39. × 1000.

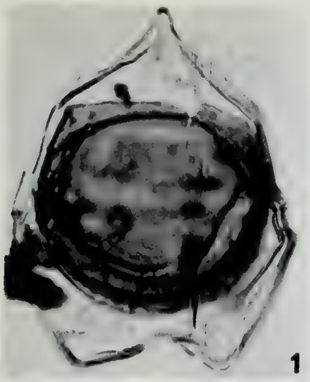
FIG. 9. Lower (dorsal) surface of same specimen showing intercalary archaeopyle. × 1000.

FIG. 12. Specimen V.57759 (17); W51. × 1000.

Phthanoperidinium alectrolophum n. sp. (p. 295)

FIG. 10. Specimen V.57791 (14); AB40. × 1000.

FIG. 11. Holotype. V.57791 (13); AB40. × 1000.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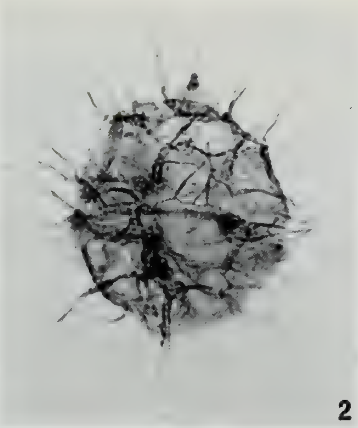
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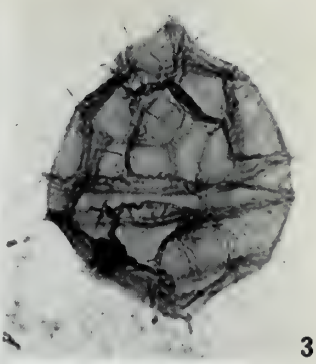
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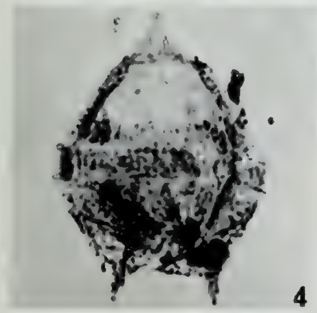
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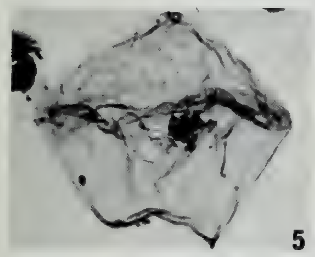
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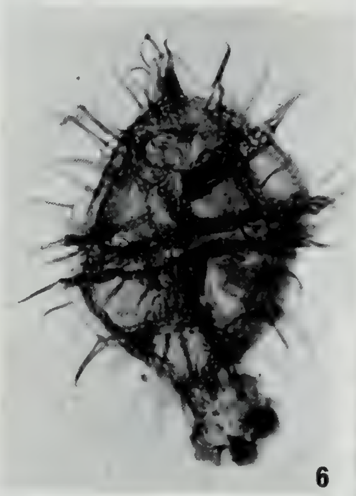
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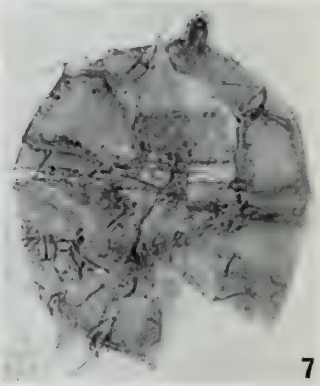
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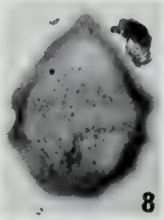
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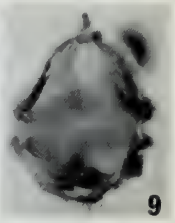
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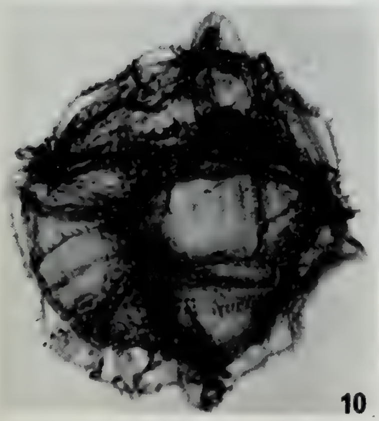
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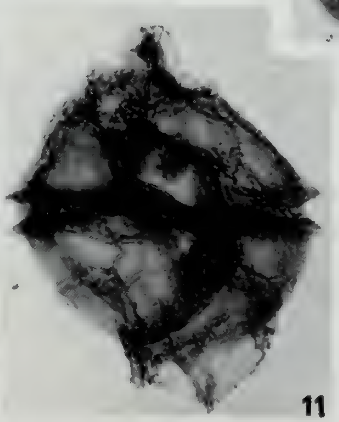
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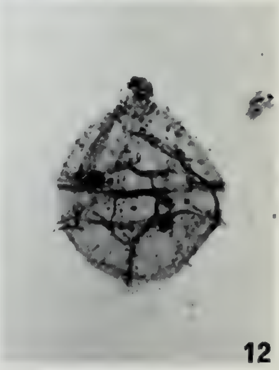
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PLATE 18

Kisselevia insolens n. sp. (p. 292)

Fig. 1. Specimen showing dorsal surface reflected tabulation. V.57775 (4) ; AB4A. × 500.

Fig. 2. Holotype V.57774 (4) ; AB4. × 500.

Wetzeliella (W.) articulata Eisenack 1938 (p. 300)

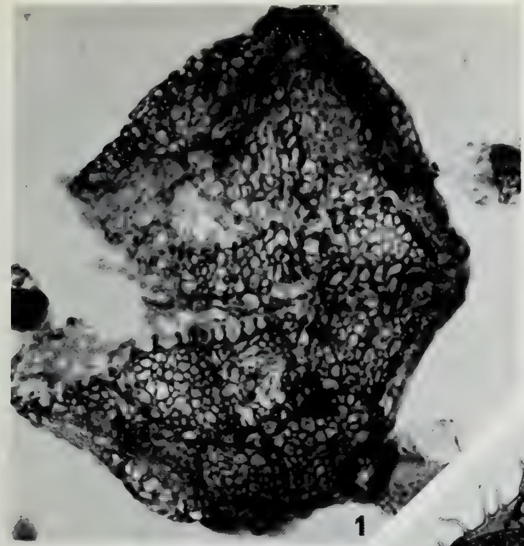
Fig. 3. Specimen showing displaced operculum within the endophragm. V.57725 ; W6. × 500.

Wetzeliella (W.) coleothrypta Williams & Downie 1966b (p. 300)

Fig. 4. Complete specimen V.57779 (2) ; AB9. × 500.

Wetzeliella (W.) condylos Williams & Downie 1966b (p. 301)

Fig. 5. Specimen showing intercalary archaeopyle. V.57726 ; W6. × 500.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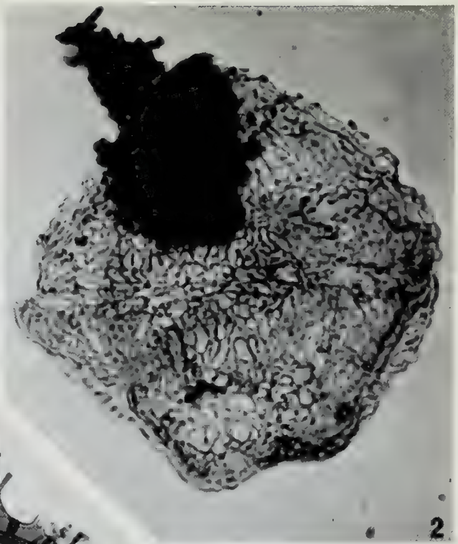
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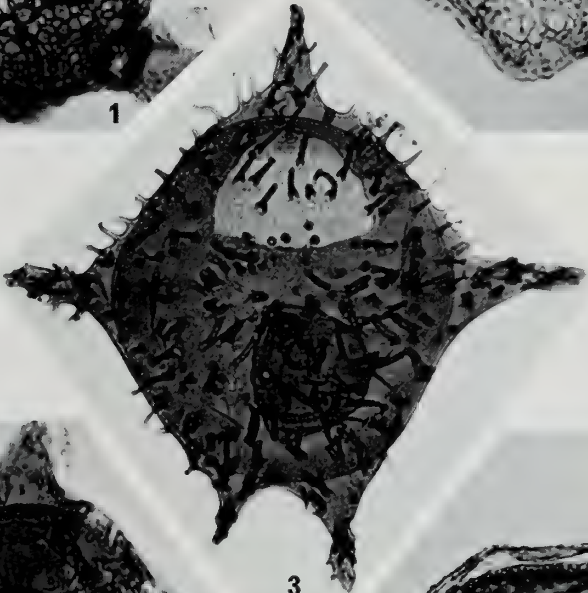
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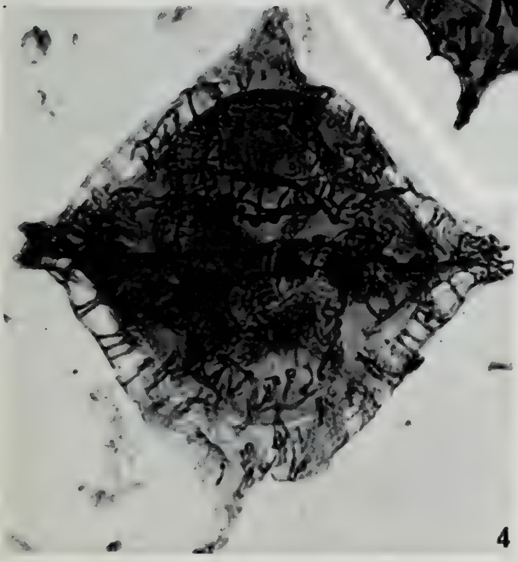
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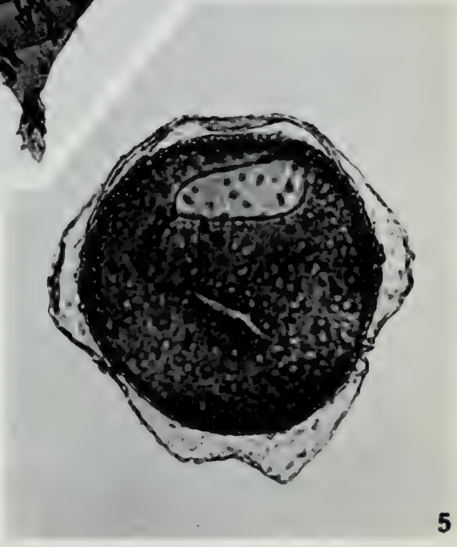
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PLATE 19

Wetzeliella (W.) homomorpha Deflandre & Cookson 1955 (p. 301)

FIG. 1. Specimen V.57785 ; AB12. × 500.

Wetzeliella (W.) lunaris Gocht 1969 (p. 302)

FIG. 2. Specimen showing characteristic reduction of one antapical horn. V.57740 ; W22. × 500.

Wetzeliella (W.) reticulata Williams & Downie 1966b (p. 302)

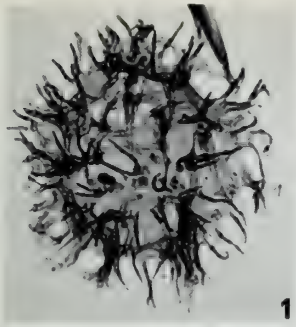
FIG. 3. Specimen V.57723 (6) ; W6. × 500.

Wetzeliella (W.) similis Eisenack 1954 (p. 303)

FIG. 4. Specimen V.57775 (5) ; AB4A. × 500.

Wetzeliella (W.) meckelfeldensis Gocht 1969 (p. 302)

FIG. 5. Specimen V.57784 (6) ; AB11. × 500.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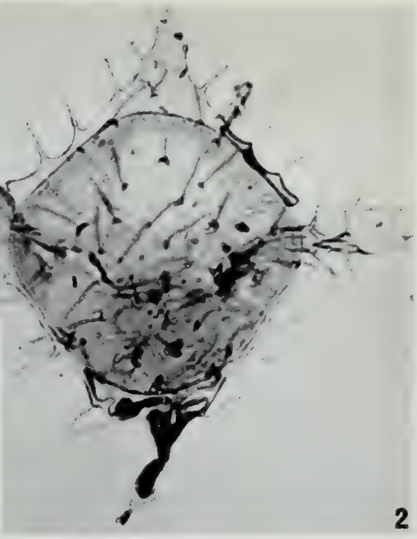
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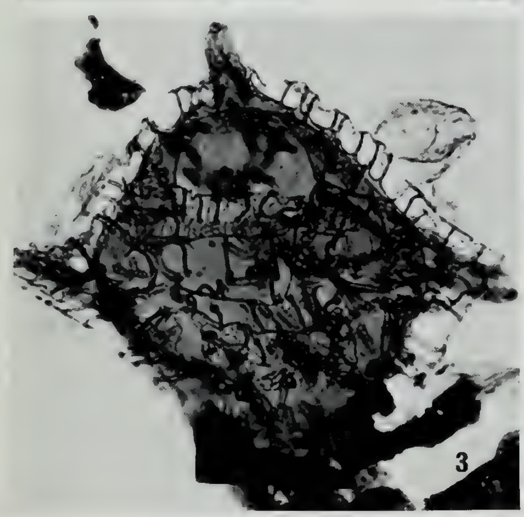
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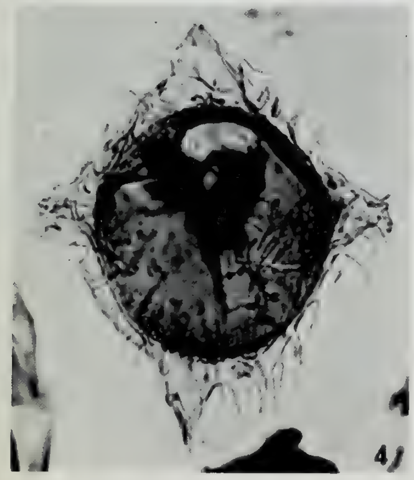
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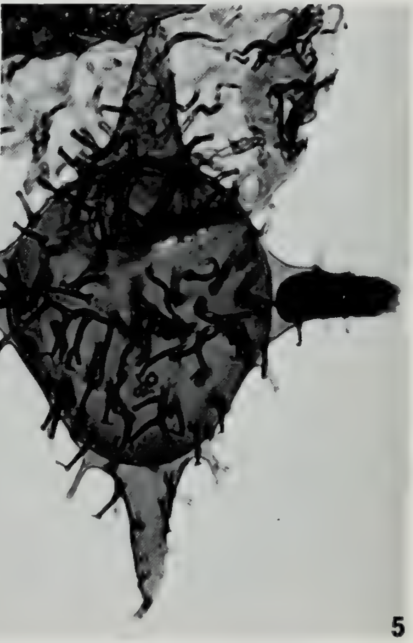
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PLATE 20

Wetzeliella (W.) tenuivirgula Williams & Downie 1966b (p. 303)

FIG. 1. Specimen showing reduced horns. V.57757 (14) ; W40. × 500.

FIG. 2. Specimen showing well-developed horns. V.57757 (15) ; W40. × 500.

Wetzeliella (W.) tenuivirgula var. ***crassoramosa*** Williams & Downie 1966b (p. 304)

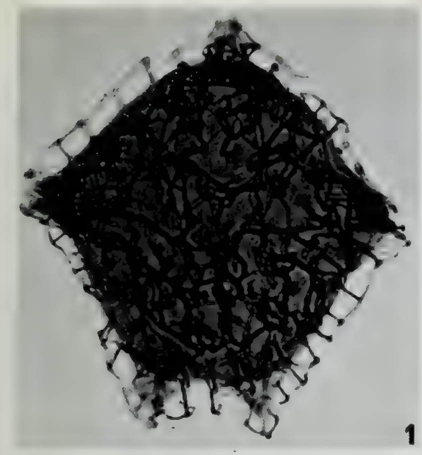
FIG. 3. Specimen V.57784 (4) ; AB11. × 500.

Wetzeliella (W.) varielongituda Williams & Downie 1966b (p. 304)

FIG. 4. Specimen V.57767 (6) ; W56. × 500.

Wetzeliella (R.) glabra (Cookson) Vozzhennikova 1967 (p. 304)

FIG. 5. Specimen showing displaced operculum. V.57731 ; W13. × 500.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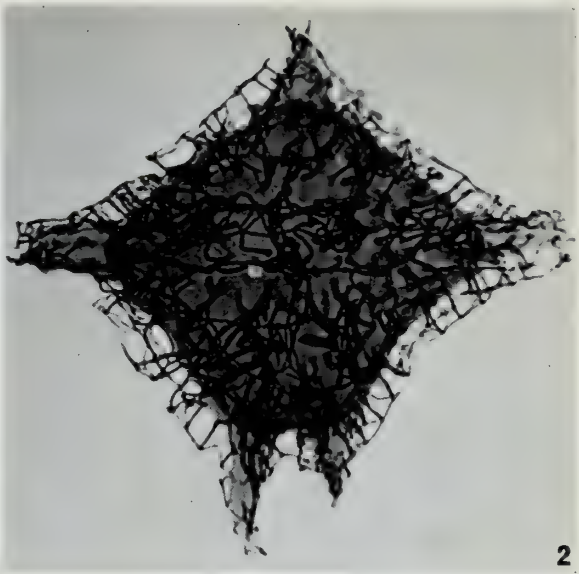
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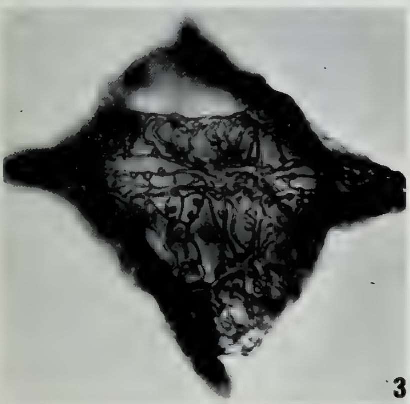
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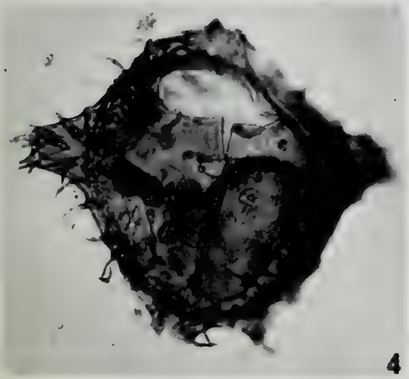
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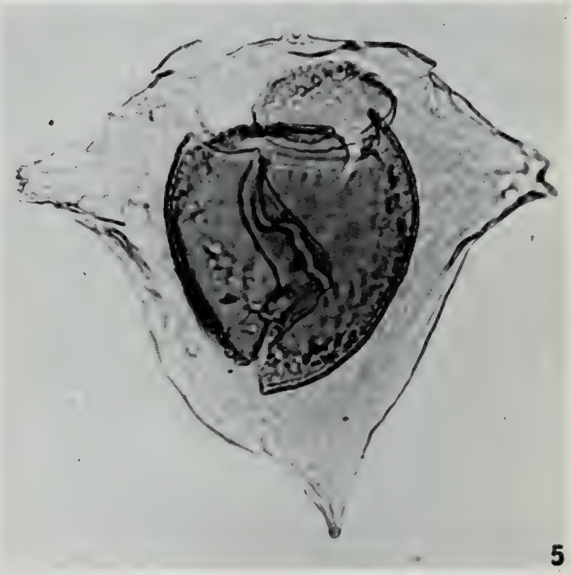
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PLATE 21

Heteraulacacysta ? leptalea n. sp. (p. 305)

Fig. 1. Holotype. V.57766 (8) ; W56. × 500.

Fig. 2. Specimen V.57766 (6) ; W56. × 500.

Impletosphaeridium luxurium n. sp. (p. 309)

Fig. 3. Holotype. V.57791 (12) ; AB40. × 850.

Fig. 4. Specimen V.57790 (4) ; AB40. × 850.

Impletosphaeridium insolitum n. sp. (p. 308)

Fig. 5. Holotype showing polygonal opening. V.57759 (13) ; W51. × 1000.

Fig. 8. Specimen V.57762 (1) ; W55. × 1000.

Impletosphaeridium cracens n. sp. (p. 306)

Fig. 6. Holotype. V.57745 (1) ; W27. × 850.

Impletosphaeridium rugosum Morgenroth 1966a (p. 309)

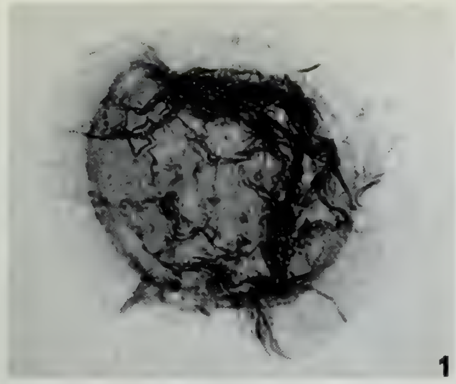
Fig. 7. Specimen V.57788 (3) ; AB28. × 850.

Impletosphaeridium kroemmelbeini Morgenroth 1966a (p. 308)

Fig. 9. Specimen V.57751 ; W36. × 850.

Impletosphaeridium implicatum Morgenroth 1966a (p. 306)

Fig. 10. Specimen V.57774 (2) ; AB4. × 850.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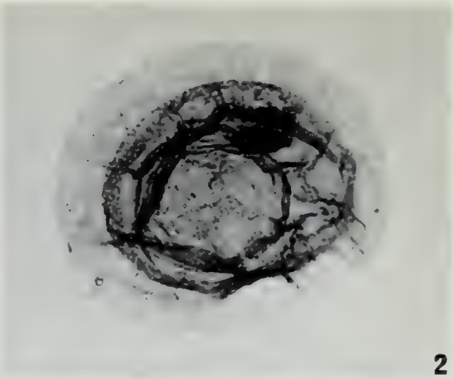
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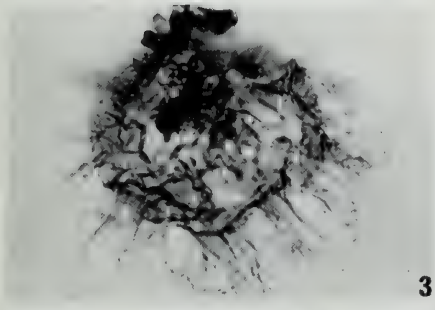
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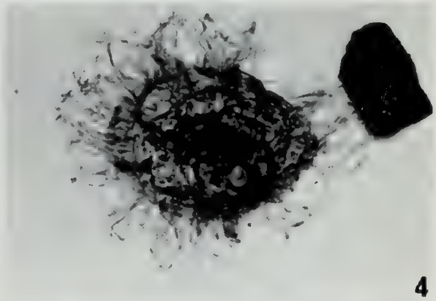
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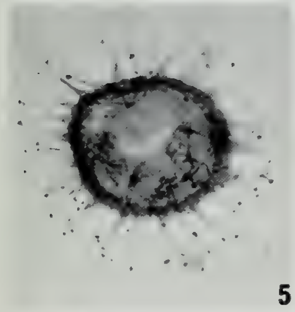
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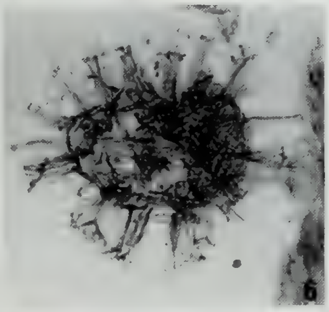
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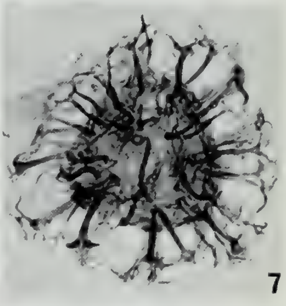
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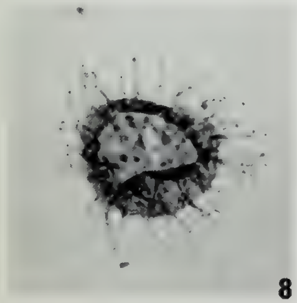
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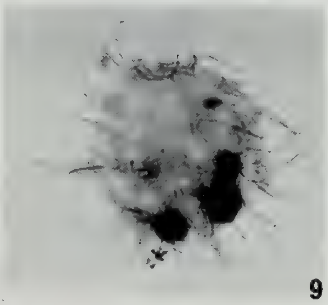
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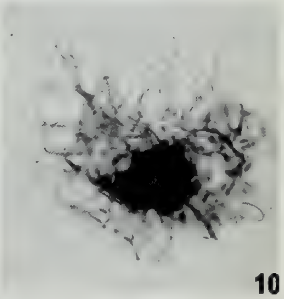
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3. Appendix. Davey, R. J., Downie, C., Sarjeant, W. A. S. & Williams, G. L. Appendix to Studies on Mesozoic and Cainozoic Dinoflagellate Cysts. Pp. 24. 1969. 95p.
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